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Performance limitations of marine mammals are analogous to those faced by autonomous underwater vehicles (AUVs). In view of this, this project evaluated key mechanisms used by an elite marine mammal, the bottlenose dolphin (*Tursiops truncatus*), to facilitate locomotor efficiency during swimming and diving. Three major mechanisms were identified, 1) intermittent propulsion during prolonged diving, 2) temporal separation of maintenance and locomotor costs, and 3) utilization of propulsion systems that permit continuous thrust production. A fourth mechanism, elastic energy storage, is under current investigation. In general, these findings suggest that cost efficiency in AUVs may be improved by incorporating intermittent duty factors into vehicle designs.

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FINAL REPORT

GRANT NUMBER: N00014-95-1-1023

PRINCIPAL INVESTIGATOR: Terrie M. Williams

INSTITUTION: University of California, Santa Cruz

GRANT TITLE: Dolphins as Models for Cost Efficient Autonomous Underwater Vehicles

AWARD PERIOD: 1 May 1995 to 30 March 2000

OBJECTIVE: To determine the key morphological, physiological and environmental mechanisms controlling locomotor efficiency in bottlenose dolphins.

APPROACH: Performance limitations of marine mammals are analogous to those faced by autonomous underwater vehicles. Both rely on efficient utilization of limited energy stores to prolong locomotor performance while submerged. Consequently, this project evaluated mechanisms used by an obligate marine mammal, the bottlenose dolphin (*Tursiops truncatus*), to increase fuel efficiency during submergence. Four major areas of investigation were undertaken, 1) identification of maximum and routine performance speeds and depths, 2) elastic energy storage, 3) intermittent propulsion, and 4) buoyancy control. Dolphins were tested both in the laboratory (Long Marine Laboratory, UCSC) and in open ocean settings (U.S. Navy Marine Mammal Laboratory, SPAWAR, San Diego; the Dolphin Experience, Freeport, Grand Bahama Island). This approach enabled a detailed examination of stroke mechanics of dolphins under controlled environmental conditions and the testing of performance limitations in freely swimming and diving animals. Laboratory measurements were conducted on nine adult bottlenose dolphins. Two animals were trained to use swimming strokes to push against a load cell at exercise loads ranging from 25 to 125 kg. Oxygen consumption, stroke mechanics, and changes in blubber deformation were correlated to level of effort to assess the role of elastic energy storage during propulsion.

Physiological and mechanical limitations to diving were determined for dolphins trained to dive to submerged targets ranging in depth from 12 to 112 m. Changes in blood oxygen, carbon dioxide and lactate were measured following each dive to assess patterns of fuel utilization. For four dolphins thermoregulatory capabilities were determined from changes in surface heat flow and skin temperature during and after submergence. These tests enabled us to determine the effects of conflicting energetic costs on efficiency. Changes in stroke mechanics and locomotor performance were examined for both shallow and deep diving dolphins. Shallow dives consisted of straight-line descents and ascents to 16 m that were videotaped by SCUBA divers with hand held cameras. For dives exceeding 20 m, stroking movements were videotaped using miniaturized instrument packs and cameras worn by the diving dolphins. Similar instrumentation was deployed on Weddell seals, elephant seals and a blue whale to provide comparative measurements for marine mammals differing in size and mode of propulsion.

ACCOMPLISHMENTS: This study successfully completed investigations on both the swimming and diving efficiency of bottlenose dolphins. One of the most important findings was the critical role of intermittent locomotion for energetic efficiency during submergence (Skrovan *et al.*, 1999; Williams *et al.*, 2000; Williams, in press). To accomplish these studies we collaborated with investigators at Texas A&M University, National Geographic, and Pisces Designs (San Diego, CA) to develop instrument packages that could be deployed on free ranging marine mammals. The units included video cameras/recorders and time-depth microprocessors in waterproof housings. These units were deployed on an adult bottlenose dolphin trained to dive to submerged targets in San Diego Bay. For comparative purposes units were also deployed on wild marine mammals including 3 adult Weddell seals diving beneath the Antarctic ice, a juvenile northern elephant seal freely diving in Monterey Bay, CA, and an adult blue whale travelling offshore of northern California. By appropriate placement of the camera we were able to record propulsive movements of the subjects throughout the dive.

The results were remarkably similar for all four species, and indicated changes in propulsive gait during the dive. Descents were characterized by prolonged periods of gliding that corresponded to changes in hydrostatic pressure and buoyancy with depth. Ascents consisted of an initial period of high amplitude constant stroking followed by burst and glide propulsion. Hydrodynamic modeling (Skrovan *et al.,* 1999) and measurements of oxygen consumption (Williams *et al*., 2000) and oxygen reserves (Williams *et al.* I, 1999) demonstrated that these changes in swimming gait during submergence resulted in a 9 - 60% reduction in energetic costs during diving when compared to dives completed by constant stroking.

Another important finding in this study was the similarity in transport costs for very different modes of propulsion in marine mammals (Williams, 1999). A single allometric regression describes transport costs for swimming marine mammals ranging in size from 21 kg to 15000 kg:

$$\mathrm{COT_{TOT}} = 7.79\mathrm{mass}^{-0.29} \qquad (r^2 = 0.83)$$

where the total cost of transport is in $\mathrm{J.kg^{-1}.m^{-1}}$ and body mass is in kg. This regression includes data for animals ranging in swimming style from dorso-ventral undulation in cetaceans to fore-flipper propulsion in otariids and lateral undulation of paired hind flippers in phocid seals. These results suggest that propulsive mode has little effect on the amount of energy expended per distance traveled as long as the animal has specialized for one form of locomotion. For example, the transport costs for semi-aquatic mammals are 2.4 – 5.1 times higher than for locomotor specialists. This is due in part to inefficient thrust-recovery modes of propulsion and to elevated body drag associated with the surface swimming position typically used by semi-aquatic mammals. In comparison to mammalian swimmers, fish show the lowest transport costs for aquatic locomotion. This difference is attributed to the higher maintenance (endothermic) costs of mammals rather than differences in the efficiency of locomotor mechanisms *per se*. Interestingly, the costs of swimming for marine mammal specialists were identical to the costs of running for similarly sized mammals specialized for terrestrial locomotion. In view of this, our findings suggest that basic mechanical and physiological principles may constrain locomotor efficiency and performance in both aquatic and terrestrial specialists. The implications of these findings are being examined in ongoing studies in our laboratory that compare the performance capabilities of locomotor specialists and generalists.

Physiological and environmental factors affecting performance in bottlenose dolphins were also examined. These studies found that marine mammals often delay or separate specific energetic costs when they compete with locomotor costs and efficiency during submergence. For example, by measuring heat flow and skin temperatures during and after diving, we found that thermoregulatory costs were often delayed until the post dive recovery period when oxygen availability was not limiting (Williams *et al.* III, 1999). A distinction in terms of energetic cost, stroking mechanics and speed of performance was found between vertical diving and horizontal swimming in exercising dolphins (Williams *et al.* I, 1999). These differences were attributed to the specific physical forces encountered by the animal. During surface swimming, wave drag was a primary force to be overcome. During diving wave drag was comparatively low, but changes in hydrostatic pressure and buoyancy affected the preferred locomotor patterns and speed of the dolphins (Williams *et al.* I, 1999; Skrovan *et al.*, 1999). These detailed examinations of energetic efficiency and energy transfer in free ranging marine mammals have been applied to broad ecological issues by other investigators. By understanding the basic energetic efficiency of marine mammals, the energetic requirements and impacts of the animals on the environment can be predicted (Estes *et al.*, 1998).

The results of these studies have also been used to broadly understand the basic mechanical and structural principles used in the design of animals for high performance, cost efficient locomotion. A generalized locomotion engineering model was developed by Rincon (2000) that described the importance of local energy storage in dictating the energetic cost of propulsion. Using data from the dolphins pushing on a load cell and freely swimming in open water, this investigator found that elastic energy transitions were a critical feature in the model. An evolutionary model describing the development of swimming efficiency in aquatic mammals was reported in Williams (1999) and demonstrated the tradeoffs between versatility and specialization in designing aquatic organisms for optimum locomotor efficiency.

Four Master's theses were completed using these data.

CONCLUSIONS: Based on these studies, we identified three major adaptations that facilitate locomotor efficiency in dolphins specifically and large aquatic mammals in general. These include

1. Changes in propulsion associated with changes in hydrostatic pressure during diving – sink or swim strategy (Williams *et al.*, 2000; Skrovan *et al.*, 1999).

2. Conservation of energy reserves by separating maintenance and propulsive costs when submerged (Williams *et al.*, 1999; Noren *et al.*, 1999).
3. Development of propulsion systems that permit thrust production throughout the stroke cycle (Williams, 1999).

A fourth mechanism that appears to play an important role in cost efficient thrust production in dolphins is elastic energy storage, and is currently being examined.

SIGNIFICANCE: These studies have provided new insights regarding mechanisms for improving locomotor efficiency in large aquatic vehicles, particularly for deployment in extreme environments. Specifically, intermittent propulsion plays a critical role in fuel efficiency for a variety of large and small marine mammals. The similarity in costs for species that differ in propulsive mechanisms indicates that specialization for one type of locomotion rather than specific propeller design is important for optimizing fuel efficiency during aquatic propulsion. The mode of propulsion (i.e. fore-flipper, lateral oscillation, dorso-ventral oscillation) undoubtedly plays a role in other features such as maneuverability, stealth and stability. Our results indicate that autonomous underwater vehicles may improve cost efficiency by incorporating intermittent duty factors into vehicle designs. The primary strategy for conserving limited on board energy stores for a wide variety of marine mammals is a reduction in the total number of propulsive events. Whenever possible the animals "turn the motor off" and preferentially rely on burst and glide, and prolonged gliding to reduce energetic costs. In addition to biomimetic applications, these results have provided information useful for the husbandry and deployment of animals in the U.S. Navy Marine Mammal program.

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Science Reprint

Sink or Swim: Strategies for Cost-Efficient Diving by Marine Mammals

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Sink or Swim: Strategies for Cost-Efficient Diving by Marine Mammals

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Locomotor activity by diving marine mammals is accomplished while breath-holding and often exceeds predicted aerobic capacities. Video sequences of freely diving seals and whales wearing submersible cameras reveal a behavioral strategy that improves energetic efficiency in these animals. Prolonged gliding (greater than 78% descent duration) occurred during dives exceeding 80 meters in depth. Gliding was attributed to buoyancy changes with lung compression at depth. By modifying locomotor patterns to take advantage of these physical changes, Weddell seals realized a 9.2 to 59.6% reduction in diving energetic costs. This energy-conserving strategy allows marine mammals to increase aerobic dive duration and achieve remarkable depths despite limited oxygen availability when submerged.

Swimming is energetically expensive for mammals and results in transport costs that are 2 to 23 times the levels predicted for fish (*1, 2*). To reduce these costs, marine mammals have developed a wide variety of energy-conserving swimming behaviors. Adherence to a narrow range of routine transit speeds (*3, 4*), wave-riding (*5*), and porpoising (*6*) decrease the amount of energy expended when pinnipeds and cetaceans move near the water surface. Although these energy-conserving strategies are especially beneficial during underwater activity, when access to ambient oxygen is limited, two of the behaviors, porpoising and wave-riding, cannot be used when the animal is submerged. In view of this, it has been assumed that marine mammals swim constantly at cost-efficient routine speeds during diving (*3, 4*). Indeed, the routine speeds of many freely diving marine mammals fall within a relatively narrow range (*7, 8*). A paradox arises when

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metabolic rates are assigned to these swimming speeds. Calculations based on measured speeds during diving and metabolic rates for bottlenose dolphins swimming near the water surface predict that the animals would be unable to complete a 200-m-deep dive using aerobic metabolic pathways. Yet, dolphins perform these dives with only small changes in postdive plasma lactate concentrations, where elevated levels would indicate a transition to anaerobic metabolism (*9*). Similar discrepancies between predicted aerobic capabilities and diving performance have been reported for a wide variety of marine birds and mammals (*10, 11*). The mechanisms by which these divers resolve the apparent conflict between the energetic demands of swimming and the conservation of limited oxygen stores during submergence are not understood (*12, 13*). Metabolic depression (*14*) and regional heterothermy (*15*) associated with cardiovascular changes during diving have been suggested, although the influence of activity level has not been assessed. This has been due in part to the difficulty of observing and monitoring diving animals at depth.

Here, we monitored locomotor behavior during diving with video cameras carried by free-ranging cetaceans and pinnipeds. Unlike other instruments placed on marine mammals in which behavior has been inferred from time-depth records or velocity profiles (*16*), video images permit direct observation of swimming periods, stroke frequency, and glide sequences. Coupled with time-depth recorders, these new tools allowed us to assess the locomotor strategies used by marine mammals throughout their dives.

Subjects for this study included three adult Weddell seals (*Leptonychotes weddellii*, body mass = 393 ± 2 kg) diving from an isolated ice hole in McMurdo Sound, Antarctica (*17*), a juvenile northern elephant seal (*Mirounga angustirostris*, 263 kg) freely diving in Monterey Bay, California (*17*), an adult bottlenose dolphin (*Tursiops truncatus*, 177 kg) trained to dive to submerged targets offshore of San Diego, California (*18*), and an adult blue whale (*Balaenoptera musculus*, estimated mass = 100 tons) traveling offshore of northern California along Cordell Bank (*19*). Each animal carried a submersible video system with a camera facing either forward to record movements of the head or backward to record propulsive movements of the flukes or hind flippers. Data loggers simultaneously monitored duration and depth of dives.

Instrumented animals were free to perform sequential dives in open water or, in the case of the Weddell seals, below the frozen sea ice. The video system and instrumentation were retrieved when the animals hauled out (Weddell seals, elephant seal) or returned to a trainer (dolphin), or the package was detached by a release mechanism (blue whale). Swimming mode, relative stroke amplitude, stroke frequency, and gliding periods were determined for each video sequence, using a motion analysis system (Peak Performance, Englewood, Colorado). These data were then matched to duration and depth of the associated dive (*20*). To assess the effect of changes in locomotor pattern on energetic costs, we measured postdive oxygen consumption of instrumented Weddell seals breathing into a metabolic hood (*21, 22*).

Despite independent evolution of swimming in cetaceans and pinnipeds, and differences in body size and propulsive mechanisms, we found a similar sequence of locomotor gaits during diving for the four species examined (Fig. 1). Diving descents began with 30 to 200 s of continuous stroking that was followed by a marked, prolonged period of gliding to maximum depth. Gliding began at similar depths (86 ± 10 m, n = 3 species) and continued to the bottom of the dive for the seals and dolphin, although maximum dive depths ranged from 115 to 385 m. The blue whale began gliding at comparatively shallower depths (18 ± 1 m, n = 3 dives) during dives of 36 to 88 m in depth. Descent rate during the glide varied little among the three smaller species (1.1 ± 0.1 m s^{-1}, n = 3 species), whereas the blue whale descended considerably slower at 0.3 to 0.4 m s^{-1}. The absolute duration of stroking or gliding sequences depended on maximum depth and dive duration. Deep divers (the phocid seals) showed the longest absolute glide periods. Maximum glide duration was 6.0 min for the juvenile elephant seal descending to nearly 400 m and 6.2 min for an adult Weddell seal descending to 540 m.

Initial ascent of each dive was characterized by sequential, large-amplitude strokes. The range of frequencies during steady stroking on initial ascent was 60 to 110 strokes min^{-1} (1.0 to 1.8 Hz) for the three smaller species (dolphin, elephant seal, Weddell seal). In comparison, the range of stroke frequencies was one-tenth of this range (6 to 10 strokes min^{-1}; 0.1 to 0.2 Hz) for the massive blue whale. Ascent rate during the period of constant stroking was 1.0 ± 0.2 m s^{-1} for all four species examined.

Following the period of continuous stroking, the animals switched to stroke-and-glide swimming for the remainder of the ascent except for a short (<100 s) glide to the surface. Only the Weddell seals did not glide the final 10 m to the surface, a behavior that was undoubtedly influenced by the presence of the sea ice and the maneuvering required to reach the isolated ice hole.

The similarity in locomotor behaviors for these four species is striking given the ranges of body sizes and propulsive mechanisms. Both cetaceans use dorsoventral undulations of a lunate tail for propulsion (*23*). The two pinniped species swim with alternate lateral sweeps of paired hind flippers in which the posterior half of the body may flex (*24*).

Passive gliding by the seals and dolphin began at nearly identical depths, suggesting that changes in hydrostatic pressure and buoyant forces prompted the incorporation of prolonged glide sequences during descent. Previous stud-

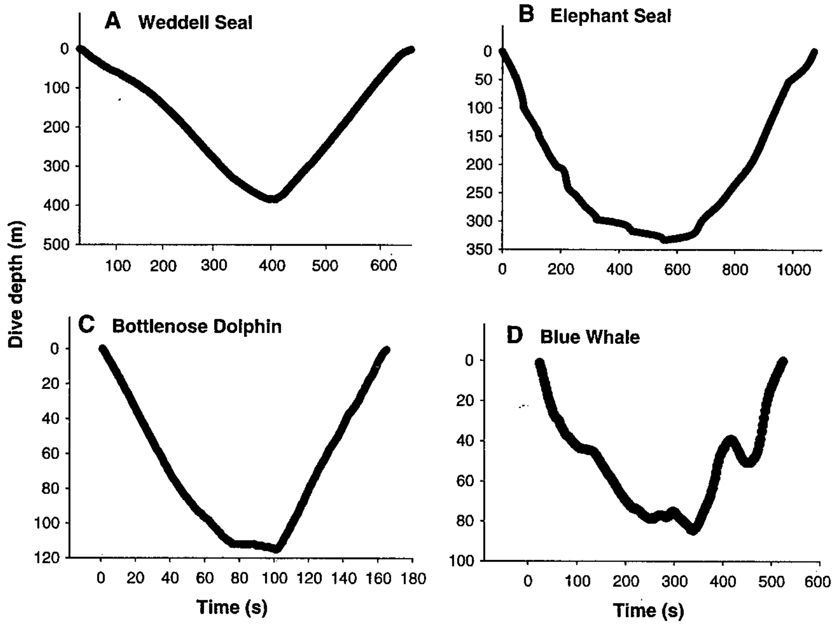

Fig. 1. Locomotor activity of four species of diving marine mammal. Representative deep dives are presented for the (**A**) Weddell seal (maximum depth = 385 m), (**B**) northern elephant seal (333 m), (**C**) bottlenose dolphin (115 m), and (**D**) blue whale (84 m). Each curve represents dive depth in relation to time elapsed during the dive. Color of the line corresponds to stroking (black) and gliding (red) periods. Stroking periods include both continuous stroking and stroke-and-glide activities. Note the prolonged gliding period during descent for each species.

ies have shown that bottlenose dolphins (*25*) and elephant seals (*26*) modify ascent and descent rates during deep dives in response to changes in buoyancy. In dolphins diving to 100 m, the magnitude of the buoyant force changes from positive (+24.3 N) near the water surface to negative (–25.7 N) at depths exceeding 67 m (*25*). These changes are attributed to the gradual collapse of the lungs and a decrease in lung volume that occur with increasing hydrostatic pressure during descent. Complete collapse of the alveoli occurs once dolphins have reached pressures equivalent to 65 to 70 m in depth (*27, 28*). Likewise, the morphological structure of the respiratory system of elephant seals and Weddell seals indicates the capacity for collapse that may affect buoyancy during the course of a dive (*29, 30*). Because compression of the air spaces decreases the volume of the animal without a change in mass, buoyancy decreases on descent. When the downward force of negative buoyancy exceeds drag forces, the animal may glide passively during descent, thereby avoiding the energetic costs associated with active stroking.

As might be expected, dive depth, and therefore distance traveled, affects the percentage of time available for gliding. The percentage of time spent gliding during descent increased significantly ($n = 53$, $r^2 = 0.70$, $P < 0.001$) and nonlinearly with increasing dive depth (Fig. 2). This percentage ranged from 10 to 63% for shallow dives of less than 100 m and reached a plateau of 82 ± 2% ($n = 21$) for deep dives exceeding 200 m. All deep dives were by the phocid seals. Blue whales also showed extended gliding sequences that exceeded 78% of the descent period for dives to 88 m.

A reduction in locomotor effort afforded by gliding should be manifested as a decrease in energetic cost. This has been reported for short-duration glides associated with intermittent (stroke-and-glide) locomotion in fish (*31*) and diving birds (*32, 33*). We found a similar result for Weddell seals that incorporated prolonged glides during diving (Fig. 3). Oxygen consumption during the recovery periods of individual dives was measured for three adult, free-ranging seals wearing video instrumentation (*21, 22*). Two groups of dives covering similar distances but differing in gliding and swimming behaviors were compared (*34*). Dives incorporating gliding during descent resulted in a 9.2 to 59.6% (mean = 27.8 ± 5.5%, $n = 10$) reduction in recovery oxygen consumption compared with dives using stroke-and-glide or continuous swimming. In general, greater savings occurred with deep dives, which is consistent with the increase in the proportion of time gliding with depth (Fig. 2). In view of these results, there appears to be a significant energetic advantage to gliding rather than swimming on descent by marine mammals.

The value of the energetic savings is demonstrated by examining the effect on the oxygen reserves of the diving seal. A 400-kg Weddell seal stores 87 ml of O_2 per kg of body weight (ml O_2 kg^{-1}) in its lungs, blood and muscle to support aerobic metabolism while submerged (*10, 11*). An average energetic savings of 27.8% (Fig. 3) due to prolonged gliding represents 24.2 ml O_2 kg^{-1}. The metabolic rate of Weddell seals during rest or low levels of underwater activity was 3.2 ml O_2 kg^{-1} min^{-1}. At this metabolic rate, the oxygen saved by gliding allows the seal to extend its aerobic dive time by 7.5 min (24.2 ml O_2 kg^{-1} divided by 3.2 ml O_2 kg^{-1} min^{-1}) assuming the same level of activity. This additional time represents 38% of the routine 20-min dive duration of free-ranging Weddell seals. The energetic savings could make the difference between completing a dive aerobically or relying on anaerobic metabolism with the coincident disadvantages associated with the accumulation of lactate and prolonged recovery (*10, 11*). For marine mammals that are hunting, these savings may increase the overall efficiency of foraging. During traveling, the energetic savings when submerged may reduce the cost of long-distance migrations.

The ability of marine mammals to take advantage of physical changes at depth permits the conservation of limited oxygen stores during submergence. These results provide insight into the means by which diving marine mammals resolve the conflict between the energetic demands of swimming and the need for energy conservation during submergence. Prolonged gliding behavior by diving marine mammals appears to be a general phenomenon, irrespective of the method of propulsion and size of the animal. Even the largest mammalian diver, the blue whale, displays this behavior.

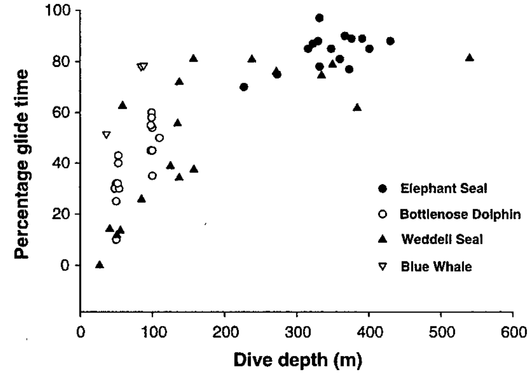

Fig. 2. Percentage glide time during descent in relation to dive depth for four species of marine mammal. Each point represents an individual dive. The data were described by the nonlinear function, percentage glide time =

$$85.9 - \left(\frac{2820.3}{\text{Depth}}\right)$$

($n = 53$, $r^2 = 0.70$, $P < 0.001$). Except for the dolphins, the range of depths was determined by the free-ranging behavior of the instrumented animals.

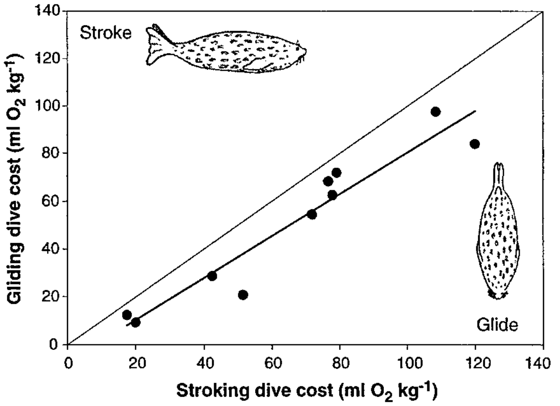

Fig. 3. Recovery oxygen consumption of gliding dives in relation to stroking dives for free-ranging Weddell seals (*34*). Each point represents a gliding dive paired with a stroking dive of equal distance traveled (±60 m) for an individual seal. Total distance traveled ranged from 354 to 3614 m, which resulted in the range of energetic costs. The thin line through the origin represents the line of equality for the cost of gliding dives and stroking dives. The thick solid line denotes the least-squares linear regression through the data points. Dives incorporating prolonged gliding were consistently less costly than stroking dives of similar distance, as described by glide cost = 0.88 stroke cost – 7.30 ($n = 10$, $r^2 = 0.91$, $P < 0.001$). Consequently, all paired dives fell below the line of equality.

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18. The experimental setup and instrumentation for the dolphin studies are described in (*25*). The instrument pack was neutrally buoyant and weighed 8 kg in air. Twenty experimental dives from 50 to 110 m were conducted in open water.
19. Blue whale studies used CRITTERCAM instrumentation (*36*) attached with a low-profile silicon suction cup (22 cm diameter). The cup released after a predetermined interval through the dissolution of a corrosible magnesium plug. The blue whale (length = 22 to 25 m) had been individually identified photographically during 1990–98 along the California coast. It was considered an adult of at least 10 years in age.
20. Gliding was defined as periods exceeding 3 to 12 s in which no locomotor movements occurred and flippers or flukes were aligned along the body axis. Deployments involving forward-facing cameras on Weddell seals also used a tail-mounted ±2-g, single-axis accelerometer (Ultramarine Instruments, Galveston, TX) to assess stroking activity. Head movements of the blue whale were considered indicative of stroke activity because of counter movements of the head and tail in swimming cetaceans (*25, 37*). Videotapes were reviewed at normal speed, except for the blue whale; cycling rate was increased sevenfold to facilitate analyses of the exceptionally slow movements of the whale.
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THE DIVING PHYSIOLOGY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

I. BALANCING THE DEMANDS OF EXERCISE FOR ENERGY CONSERVATION AT DEPTH

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Summary

During diving, marine mammals must rely on the efficient utilization of a limited oxygen reserve sequestered in the lungs, blood and muscles. To determine the effects of exercise and apnea on the use of these reserves, we examined the physiological responses of adult bottlenose dolphins (*Tursiops truncatus*) trained to breath-hold on the water surface or to dive to submerged targets at depths between 60 and 210 m. Changes in blood lactate levels, in partial pressures of oxygen and carbon dioxide and in heart rate were assessed while the dolphins performed sedentary breath-holds. The effects of exercise on breath-hold capacity were examined by measuring heart rate and post-dive respiration rate and blood lactate concentration for dolphins diving in Kaneohe Bay, Oahu, Hawaii. Ascent and descent rates, stroke frequency and swimming patterns were monitored during the dives. The results showed that lactate concentration was 1.1±0.1 mmol l^{-1} at rest and increased non-linearly with the duration of the sedentary breath-hold or dive. Lactate concentration was consistently higher for the diving animals at all comparable periods of apnea. Breakpoints in plots of lactate concentration and blood gas levels against breath-hold duration (P_{O_2}, P_{CO_2}) for sedentary breath-holding dolphins occurred between 200 and 240 s. In comparison, the calculated aerobic dive limit for adult dolphins was 268 s. Descent and ascent rates ranged from 1.5 to 2.5 m s^{-1} during 210 m dives and were often outside the predicted range for swimming at low energetic cost. Rather than constant propulsion, diving dolphins used interrupted modes of swimming, with more than 75 % of the final ascent spent gliding. Physiological and behavioral measurements from this study indicate that superimposing swimming exercise on apnea was energetically costly for the diving dolphin but was circumvented in part by modifying the mode of swimming.

Key words: dolphin, *Tursiops truncatus*, diving, heart rate, energetics.

Introduction

Previous studies have demonstrated that swimming dolphins modify their energetic costs by altering their mode of locomotion. Porpoising (Au and Weihs, 1980; Blake, 1983a), wave-riding (Williams et al., 1992) and travelling at energetically efficient routine speeds (Williams et al., 1993a,b) are behavioral options that significantly lower locomotor costs in these animals during transit swimming near the water surface. Diving poses a unique challenge to locomotion because of changes in pressure with depth. On especially long dives, small dolphins will take advantage of these pressure changes and switch from constant propulsion to interrupted patterns of swimming (Skrovan et al., 1999). Although the energetic benefits of this behavior have not been determined for marine mammals, alternating periods of accelerated motion and powerless gliding have been found to increase the swimming efficiency of other streamlined aquatic vertebrates (Weihs, 1974). For example, the predicted cost of swimming may be reduced by as much as 50 % in some species of fish that utilize interrupted swimming patterns in comparison with those using steady swimming at the same average velocity (Weihs, 1974; Videler and Weihs, 1982).

Energetically efficient modes of swimming by marine mammals are especially important during diving when access to oxygen is limited to reserves sequestered in the lungs, blood and muscles (Kooyman, 1989). Lower locomotor costs in diving marine mammals potentially provide the added advantage of parsimoniously utilizing oxygen reserves and, hence, prolonging aerobic metabolic support during submergence. For the foraging aquatic mammal, the result may be realized as an increase in the time available for locating and capturing prey (Dunstone and O'Connor, 1979; Kramer, 1988).

The demand for energy conservation will probably depend on the duration and depth of the dive. Diving cetaceans, like other marine mammals, must balance metabolic demands associated with supporting exercise while conserving a limited oxygen store (Castellini et al., 1985; Hochachka, 1986). Short-duration dives, compared with longer dives, presumably permit greater flexibility in speed and swimming mode because the relative impact on oxygen stores is lower. Longer dives in which oxygen reserves become limiting should result in the expression of energy-conserving strategies by the animal (Williams et al., 1996). Consequently, dolphins may tailor their mode of propulsion, routine speed and coincident energetic costs to match specific tasks or when performing longer dives.

This study examines the physiological responses and locomotor strategies of adult, bottlenose dolphins *Tursiops truncatus* performing long- and short-duration dives. To differentiate between responses associated with apnea alone and with apnea during submerged exercise, the study was divided into two parts; sedentary breath-holding on the water surface, and open-ocean diving. Plasma lactate concentration, heart rate and partial pressure of oxygen and carbon dioxide in the blood were determined during apnea on the water surface. We also monitored swimming style, heart rate and post-dive lactate production and respiration rate in dolphins trained to dive to submerged buoys positioned at a depth of 60–210 m. These results were compared with the maximum exercise response of dolphins during stationary exercise pushing against a force transducer and transit swimming on the water surface (Williams et al., 1993a). The results show a graded diving response that correlated with swimming activity, dive depth and duration of submergence. Energy-conserving modes of locomotion appear to slow the rate of oxygen utilization and, consequently, extend dive duration. This strategy is more apparent for longer, deeper dives than for relatively short dives.

Materials and methods

Animals

Three adult, female Pacific bottlenose dolphins (*Tursiops truncatus gilli* Gervais, 1855) were used in sedentary breath-hold studies and open-water diving tests. An additional male, hybrid (*Tursiops truncatus gilli* × *Tursiops truncatus truncatus*) was also used in the open-water tests. The mean body mass of the dolphins was 197.5±17.8 kg (mean ± S.D.). The animals were housed in floating pens (7 m×7 m×3 m deep) in a saltwater bay and were fed 2–3 times daily on mackerel, herring and smelt supplemented with vitamins. Mean water temperature in the pens during the experimental period was 24.6±1.20 °C (mean ± S.D.).

Experimental design

The dolphins were studied under two experimental conditions: (1) sedentary breath-holding on the water surface, and (2) voluntary diving in open water. Surface breath-hold tests were conducted to determine the effect of apnea alone on physiological responses. Serial blood samples taken during these tests were used to assess the relationships between voluntary breath-hold duration, blood gas levels, lactate concentration and blood pH. Open-water diving sessions assessed the combined effects of exercise and apnea on heart rate, muscle lactate production and post-dive respiration rates. Dives were conducted in Kaneohe Bay and along Mokapu Peninsula on Oahu, Hawaii. To avoid prolonged swimming exercise before the diving trials, the dolphins were transported in a 21 foot motorboat (Boston Whaler) to a predetermined dive site. The boat was stationed over a submerged buoy using a hand-held global positioning system (GPS) unit. The dolphins performed straight-line dives to a buoy anchored on the bottom and returned directly to the boat. Diving depths ranged from 60 to 210 m.

Sedentary breath-holding

The dolphins were trained using standard operant conditioning techniques to station next to a deck and to bite onto a padded mouthpiece mounted on a strut. The mouthpiece swiveled, enabling the resting dolphin to be inverted with its closed blowhole under water. This position ensured that the dolphin remained in breath-hold and provided access to blood vessels on the ventral fluke. Following a preparatory breath, the dolphin was inverted, and a butterfly catheter (21 gauge × 3/4 inch) was inserted into the fluke vein. Blood samples were drawn anaerobically into heparinized syringes (10 ml) at 1 min intervals for the duration of the breath-hold. If air bubbles were detected in the catheter line or syringe, the sample was discarded. Capped syringes were placed in an ice slurry and processed immediately. Each sample was analyzed for pH and for the partial pressures of oxygen and carbon dioxide. In addition, plasma lactate concentration was determined for the final sample of each session (see below).

Care was taken to avoid a forced dive response by training the animals for voluntary breath-holds (Ridgway et al., 1975). Behavioral conditioning for the breath-hold tests occurred over several months, as described by Shippee et al. (1994). The dolphins determined the duration of each breath-hold session by biting onto or releasing the mouthpiece. Voluntary breath-holds ranged from 1 to 6 min. The difference between a forced or voluntary breath-hold response was assessed from changes in heart rate (described below). A heart rate below 10 beats $\min^{-1}$ was considered indicative of a forced dive response (Elsner et al., 1966; Kooyman, 1989). After training, heart rates for the dolphins during the breath-hold tests remained above 30 beats $\min^{-1}$ and were similar to levels recorded during voluntary open-ocean diving.

Open-ocean diving

Dolphins were transported by boat to a dive site within 8 km offshore of Oahu, Hawaii. Once released into the water, the animals stationed next to the boat so that a harness could be attached. Each dolphin carried one of two instruments during the dive sessions. The first was a time/depth recorder (1.3 cm×3.7 cm×6.2 cm; Wildlife Computers, Inc., Woodenville, WA, USA) mounted onto a pectoral fin strap (1.9 cm nylon ribbon padded with polyvelvet cloth). This instrument recorded changes in depth and water temperature at 1 s intervals throughout the dive. The recorder was pressure-tested to 450 m before and after the experimental period and was accurate to ±2 m. During sessions in which heart rate was monitored, a second instrument that recorded heart rate as well as time and depth was attached to a mid-thorax harness (see below).

The dolphins were trained to dive in a straight-line path between the boat and a buoy. Respiratory rate was monitored for 1 min periods immediately following each dive. A blood sample was subsequently drawn from the ventral fluke vein for determination of lactate concentration. Training the animals to present their flukes voluntarily for sampling facilitated blood collection. Using this technique, we obtained the samples within 2–4 min after completion of the dive. Previous experiments in which serial blood samples were taken demonstrated that peak lactate concentrations were obtained during this period (Williams et al., 1993a). Test tubes containing whole blood samples were placed in an ice slush and delivered to the laboratory within 1 h. Data from the microprocessors were downloaded to a personal computer following each diving session and analyzed for average descent and ascent rates, dive duration and dive depth.

Blood gas levels, pH and lactate concentration

The pH and partial pressures of oxygen and carbon dioxide (P_{O_2}, P_{CO_2}) were determined from whole-blood samples of sedentary breath-holding dolphins. The blood gas analyzer (158 pH/blood gas analyzer, Ciba-Corning) was calibrated daily, and the electrode membranes were changed immediately before each experimental session. Buffer calibration standards ranged from pH 6.84 to pH 7.38. Gas standards ranged from 0 to 10 mol % for CO_2 and from 0 to 12 mol % for O_2. All measurements were made at 37 °C.

Plasma lactate concentration was determined for blood samples taken from both the sedentary breath-holding and open-ocean diving dolphins. Chilled samples (10–12 ml in heparinized vacutainers; Becton Dickinson) were centrifuged (approximately 1000*g* for 10 min), and the plasma was analyzed for total lactate concentration (YSI Industrial Analyzer, model 27, and Kodak Ektachem 700C). The analyzers were calibrated daily with lactate standards ranging from 0 to 133.6 mg dl^{-1} (0–15.0 mmol l^{-1}).

Heart rate

An electrocardiograph (Birtcher Heart Rate Monitor, model 365) and a heart rate/dive depth microprocessor (2.5 cm diameter × 15 cm long; Wildlife Computers, Inc.; Woodenville, WA, USA) were used to monitor the heart rate of sedentary and diving dolphins, respectively. Electrocardiograph (ECG) signals were monitored continuously during four breath-hold tests using two cross-thorax surface electrodes placed on the sternum between the pectoral fins and on the mid-lateral axillary area. Each electrode consisted of a 3.0 cm diameter silver plate mounted in an 8.5 cm suction cup. Insulated wires from the electrodes were connected to the monitor and recorded ECG signals at 2.5 cm s^{-1}.

The nylon harness used to carry the heart rate/dive depth recorder had a streamlined, low profile (<5 % of the frontal area of the dolphin) designed to minimize drag (Culik and Wilson, 1991). Previous open-water swim tests with the dolphins demonstrated that there was no significant difference in physiological responses (respiration rate and blood lactate) with and without the harness at speeds up to 2.9 m s^{-1} (Williams et al., 1993a). Therefore, we assumed that there was little additional energetic cost associated with the harness at relatively low speeds during diving.

Heart rate was averaged for 10 s intervals throughout the dive and for 2 min periods before and after each dive. Dive depth and duration were recorded simultaneously by the microprocessor at 1 s intervals. Following each dive session, the data were downloaded to a personal computer. Changes in heart rate in relation to dive depth and duration were determined using Dive-Analysis (Wildlife Computers, Inc.; Woodenville, WA, USA). To ensure the accuracy of the heart rate microprocessor and electrode sensitivity, we periodically tested average heart rates from the microprocessor against values determined from ECG waveforms (Birtcher heart rate monitor, model 365) for dolphins resting on the water surface.

Breath-hold duration and respiratory rate

Sedentary breath-hold duration, respiratory rate and dive duration of the dolphins were recorded by observers with stopwatches. Mean respiratory rate was determined by counting the total number of inspirations for 1 min periods immediately following each dive and during resting in saltwater pens.

Swimming mode during diving

During open-water dive sessions, a hand-held video camera (Canon model H680 in an Ewa Marine Aqua-Video housing) was used to record the first 25 m of the dolphins' descent and the final 25 m of ascent. Water clarity and SCUBA limits of the human divers dictated the depth range of recording. The video tapes were analyzed for swimming mode (continuous or interrupted dorso-ventral undulation), stroke frequency and percentage of time spent gliding. Stroke frequency was calculated as the total number of strokes divided by the recorded ascent or descent interval. Gliding was defined as forward movement of the animal while the flukes were positioned in line with the lateral axis of the body (Lang, 1966). The percentage of time spent gliding was calculated from the sum of the durations of the glide periods divided by the duration of the ascent or descent recorded.

Statistical analyses

Data for heart rate, respiratory rate, blood gas levels, plasma lactate concentration and stroke frequency are presented as mean ±1 standard error of the mean (S.E.M.). Differences between means were tested using Student's *t*-tests according to Zar (1974). Linear and non-linear relationships were calculated by least-squares procedures using statistical software (Sigma Stat 2.0, Jandel Scientific, Inc.). Best-fit correlations for individual relationships are presented. Critical breakpoints in the data were used to assess the relationship between the calculated aerobic dive limit and changes in post-dive plasma lactate accumulation and blood gas levels. Breakpoints for the relationships between breath-hold duration and blood gas levels and between dive duration and plasma lactate concentration were defined from the intersection of multiple regressions using Yeager and Ultsch (1989). Low sample number prevented the critical breakpoint for plasma lactate concentration in relation to the duration of sedentary breath-holding from being determined. Heart rate was calculated by dividing the total number of ECG waveforms or fractions thereof by the test interval according to Chabot et al. (1989).

Results

Sedentary breath-holding

Blood gas levels and pH

Partial pressures of oxygen (P_{O_2}) and carbon dioxide (P_{CO_2}) in mixed venous blood samples showed linear relationships with breath-hold durations up to 225 s (Fig. 1); longer durations were characterized by a decline in the rate of change in the partial pressure of the gases. P_{O_2} decreased with breath-hold duration (t_B) and is described by the equation:

$$P_{O_2} = 58.5 - 0.16t_B \quad (1)$$

(N=13, r^2=0.70, P<0.001) for breath-holds less than 225 s, where P_{O_2} is in mmHg (1 mmHg=0.133 kPa) and breath-hold duration is in seconds. The relationship between P_{O_2} and breath-hold duration for the period exceeding 240 s is:

$$P_{O_2} = 32.8 - 0.03t_B \quad (2)$$

(N=9, r^2=0.08, P=0.45), but was not statistically significant. This gas averaged 25±2 mmHg (N=9) with breath-hold durations of 240 s or longer. In contrast, P_{CO_2} increased linearly with breath-hold durations up to 225 s. The least-squares linear regression for this relationship is:

$$P_{CO_2} = 47.7 + 0.06t_B \quad (3)$$

(N=14, r^2=0.64, P<0.001), where P_{CO_2} is in mmHg. As observed for P_{O_2}, a breakpoint occurred in the relationship between P_{CO_2} and breath-hold duration for periods exceeding 240 s. The relationship for longer breath-hold durations is:

$$P_{CO_2} = 52.2 + 0.02t_B \quad (4)$$

(N=8, r^2=0.21, P=0.254). Mean P_{CO_2} for breath-holds exceeding 240 s was 60±1 mmHg (N=8). Blood pH was independent of breath-hold durations ranging from 60 to 405 s. Mean pH for all breath-hold tests was 7.34±0.04 (N=25).

Plasma lactate concentration

Plasma lactate concentration of resting Pacific bottlenose dolphins floating in water was 1.10±0.1 mmol l^{-1} (N=5). The concentration of plasma lactate increased curvilinearly with the duration of sedentary breath-holding (Fig. 2) and was described by the equation:

$$[\text{Lactate}] = 1.16 + 0.0002t_B{}^{1.5} \quad (5)$$

(N=8, r^2=0.55, P=0.138), where lactate concentration is in mmol l^{-1}. Plasma lactate concentration was 2–3 times higher than resting levels following breath-holds exceeding 300 s. However, the values were consistently lower than those measured for actively diving or exercising dolphins for comparable periods of apnea (see below).

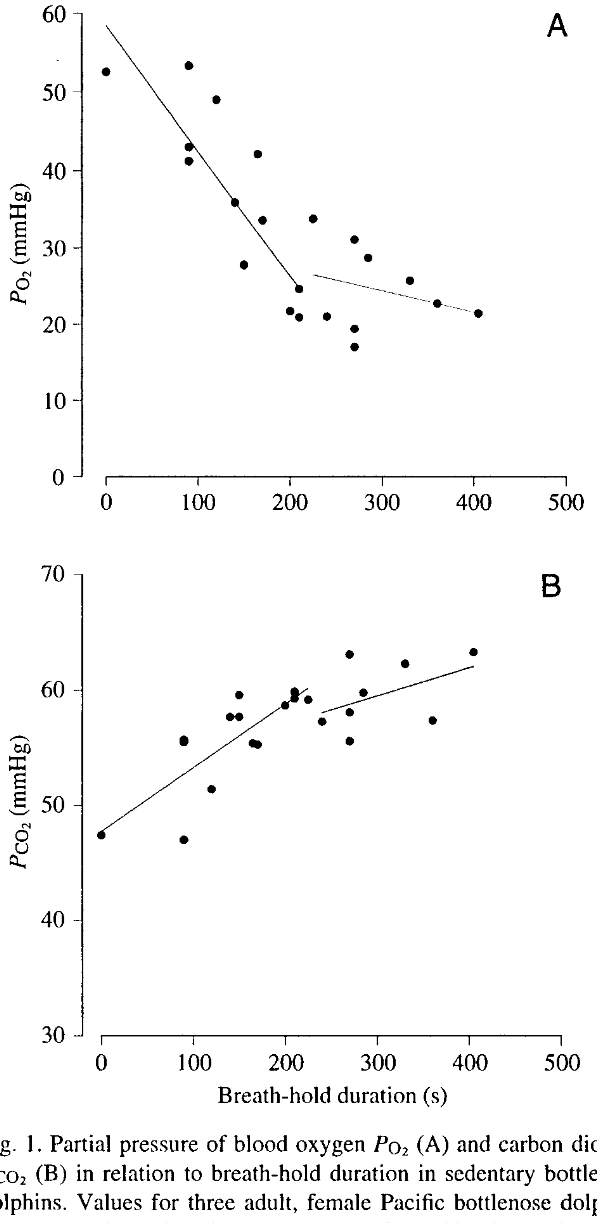

Fig. 1. Partial pressure of blood oxygen P_{O_2} (A) and carbon dioxide P_{CO_2} (B) in relation to breath-hold duration in sedentary bottlenose dolphins. Values for three adult, female Pacific bottlenose dolphins are presented. Each point represents a single blood sample. Solid lines are least-squares linear regressions for the data points. Breakpoints between regressions were determined statistically according to Yeager and Ultsch (1989). Equations and statistics are presented in the text. 1 mmHg=0.133 kPa.

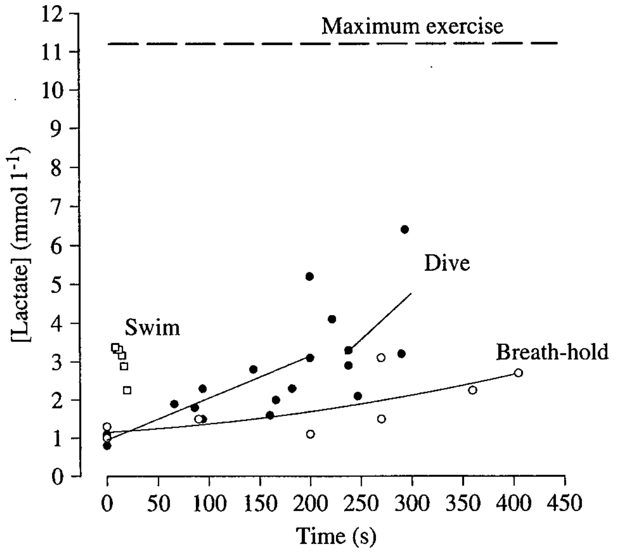

Fig. 2. Plasma lactate concentration in relation to the duration of apnea in sedentary (open circles), open-ocean diving (filled circles) and transit-swimming (open squares) dolphins. Values for four adult bottlenose dolphins are presented. Each point represents a single post-submergence blood sample. Solid lines are the least-squares linear or power regressions through the data points (see text). The upper dashed line shows the maximum plasma lactate level obtained for a dolphin during stationary exercise (Williams et al., 1993a).

Open-water diving

Heart rate

Changes in heart rate during 60 m and 210 m dives are shown in Fig. 3A and 3B, respectively. Average heart rate for the 2 min period before the shallower dives was 101.8±0.7 beats min^{-1} (N=6); the rate before the deeper dives was 111.3±2.2 beats min^{-1} (N=6). Upon submergence, the animals showed a rapid and marked bradycardia. Although the maximum response was achieved in approximately 30 s during the 60 m dives, maximum bradycardia did not occur until nearly 60 s during the 210 m dives. In addition, the final bradycardia response differed significantly (at P<0.05) between the two dive depths. Average heart rate at the bottom depth was 37.0±1.8 beats min^{-1} (N=6) for the 60 m dives and 30.0±2.2 beats min^{-1} (N=6) for the 210 m dives.

Heart rate also showed considerable variability during the ascent phase of dives at both depths. This may have been due in part to an anticipatory tachycardia during the ascent, as described for free-ranging pinnipeds (Hill et al., 1987; Fedak et al., 1988; Thompson and Fedak, 1993; Andrews et al., 1997). Average heart rate during the 2 min immediately following the dives was 6–10 % lower than pre-dive levels, although the results were not significantly different (at P>0.10). Post-dive heart rate was 95.8±5.3 beats min^{-1} (N=6) for 60 m dives and 101.1±4.2 beats min^{-1} (N=5) for 210 m dives.

Respiratory rate

The mean respiratory rate (f_V) of resting adult dolphins at the surface was 3.9+0.2 breaths min^{-1} (N=10). This rate was higher during the first minute following diving and was positively correlated with both dive depth (h) (Fig. 4A) and dive duration (t_D) (Fig. 4B). The resulting equations were:

$$f_V = 4.1 + 0.03h \qquad (6)$$

(N=25, r^2=0.71, P<0.001) and

$$f_V = 4.0 + 0.02t_D \qquad (7)$$

(N=25, r^2=0.78, P<0.001), where respiratory rate is in

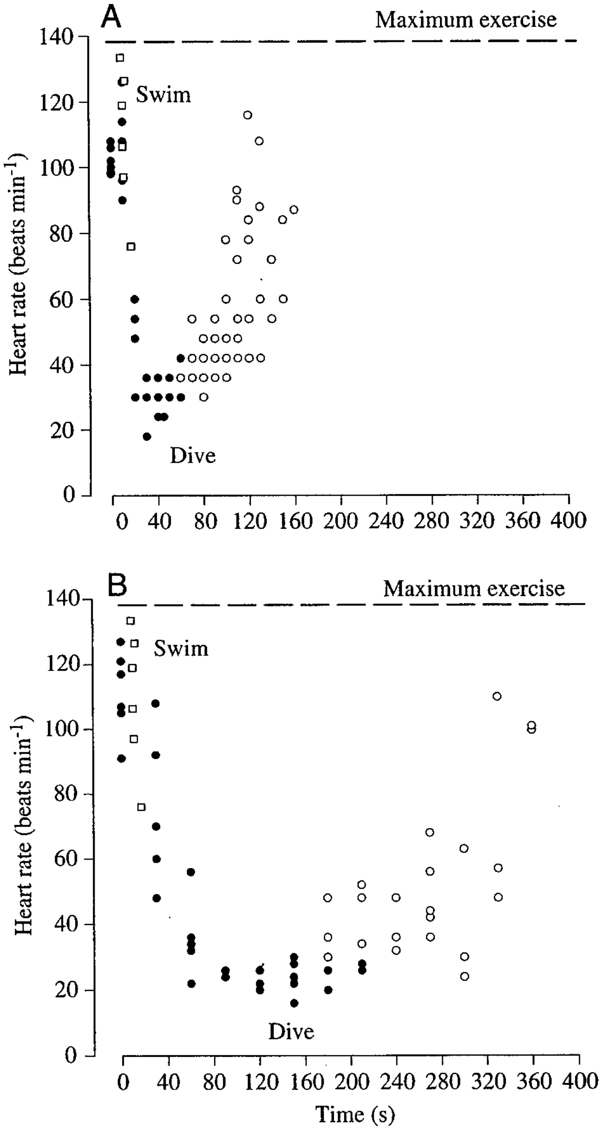

Fig. 3. Heart rate in relation to dive duration for two Pacific bottlenose dolphins. Data for six dives each at 60 m (A) and 210 m (B) are presented. Each point represents the average heart rate for a 10 s interval during the dive. Filled circles denote values for heart rate during the descent phase of the dives; open circles are for the ascent phase. Note the variability in heart rate during ascent. Average heart rate values for transit-swimming dolphins on the water surface (squares) are shown for comparison. Transit-swimming sessions were 10–25 min in duration at a constant speed ranging from 2.1 to 3.8 m s^{-1}. The upper dashed lines illustrate the maximum heart rates for bottlenose dolphins during stationary exercise (Williams et al., 1993a).

breaths min^{-1}, dive depth is in meters and dive duration is in seconds. Respiratory rate following the deepest dives examined in this study was 2.5 times the value for resting dolphins (Fig. 4A) and approached the maximum exercise rates for dolphins pushing against a load cell (Williams et al., 1993a).

Plasma lactate concentration

Plasma lactate concentration was 1.94±0.14 mmol l^{-1} (N=5) following 60 m dives and was not significantly different (at P<0.005) from resting values. Mean values for plasma lactate concentration increased with dive depth and were significantly different (at P=0.04) once depth exceeded 140 m. Lactate concentration subsequently increased to 3.76±0.52 mmol l^{-1} (N=7) following 210 m dives, representing a 3.4-fold increase over resting levels (Fig. 2).

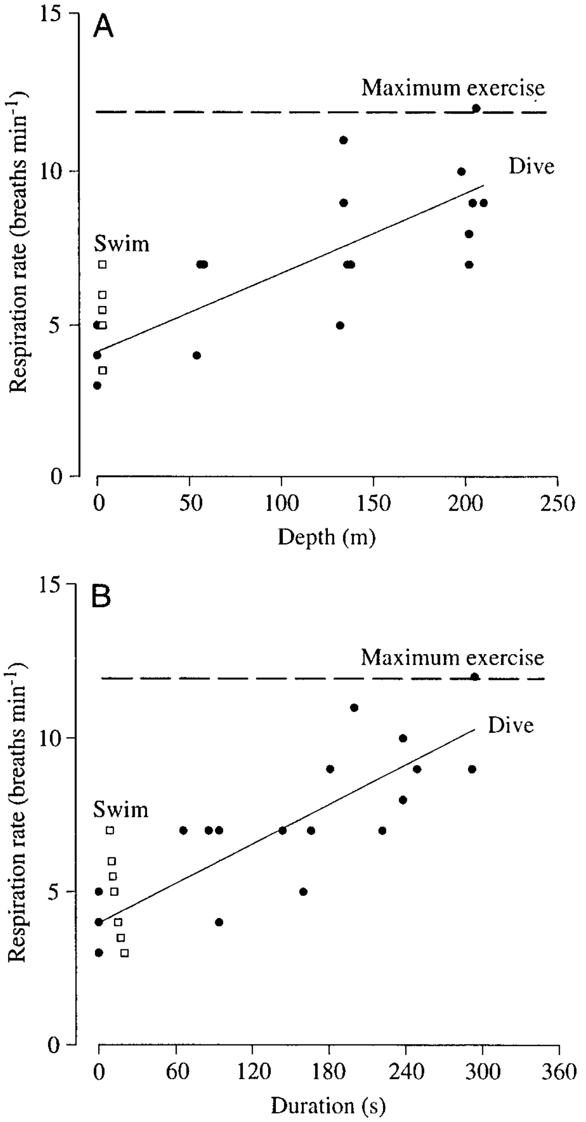

Fig. 4. Respiration rate of Pacific bottlenose dolphins in relation to dive depth (A) and dive duration (B). Each point represents a single measurement taken for 1 min at rest or immediately following a dive. Solid lines are the least-squares linear regressions through the data points. The upper dashed lines represent the maximum respiratory rate for dolphins during stationary exercise on a force transducer (Williams et al., 1993a). Statistics are presented in the text.

Post-dive lactate levels were consistently higher than those of sedentary breath-holding dolphins at comparable durations of apnea. As observed for sedentary dolphins, plasma lactate concentration increased with the duration of apnea in the diving dolphins (Fig. 2). A linear increase in concentration occurred with dives up to 200 s in duration and is described by the relationship:

$$[\text{Lactate}] = 0.95 + 0.011t_{\text{D}} \qquad (8)$$

(N=13, r^2=0.54, P=0.005), where lactate concentration is in mmol l^{-1} and dive duration is in seconds. Longer dives resulted in a breakpoint in this relationship. The relationship between plasma lactate concentration and dive duration for periods exceeding 222 s is:

$$[\text{Lactate}] = 0.024t_{\text{D}} - 2.47 \qquad (9)$$

(N=6, r^2=0.24, P=0.330). The large variability in lactate concentration following longer duration dives contributed to the low significance level for this relationship.

Diving behavior

Descent and ascent rates for diving dolphins ranged from 1.4 to 2.5 m s^{-1} (Table 1). For the two depths examined, ascent rates were more than 51 % faster than the corresponding descent rate. Assuming a straight path between the boat and submerged buoy, these rates demonstrate that the diving

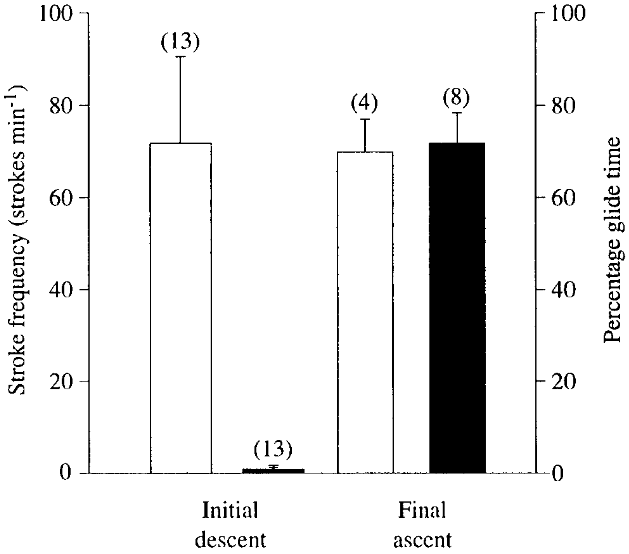

Fig. 5. Stroke frequency (open columns) and percentage glide time (filled columns) of bottlenose dolphins during the initial descent and final ascent from 210 m dives. The height of the columns and vertical lines represent the mean +1 S.E.M. Numbers in parentheses denote the total number of dives. Note that, because of visibility, data from the top 25 m of the water column only are presented.

Table 1. *Speed and duration of diving in adult Pacific bottlenose dolphins*

	Depth 60 m			Depth 210 m		
	Descent	Bottom	Ascent	Descent	Bottom	Ascent
Speed ($m\,s^{-1}$)	1.4±0.1	–	2.2±0.1	1.5±0.1	–	2.5±0.1
N	17		17	16		16
Duration (s)	44.3±3.6	10.1±1.9	25.8±0.9	131.8±4.4	29.5±5.0	82.4±2.1
N	20	20	20	16	16	16

The results for two females are presented.

Swimming speed, duration of travel and bottom time were determined from time/depth microprocessors carried by the diving animals.

Average speed of descent and ascent were calculated for each dive by dividing the straight-line transit distance between 5 m depth and a submerged target by the duration of performance.

N, the number of dives in each category. Values are means ± 1 S.E.M.

animals often moved at speeds outside the predicted range, 1.7–2.3 $m\,s^{-1}$, considered to be the most cost-efficient swimming speeds for bottlenose dolphins (Williams et al., 1993b). Average descent speed for both depths was slower than the predicted routine speed range. Ascent rate during the 210 m dives was higher than the predicted range. Both descent and ascent rates were consistently higher for 210 m dives than for shallower dives (Table 1) although the mean values were not statistically different (P=0.141 for descent, P=0.113 for ascent).

Videotaped and direct observations by SCUBA divers showed that the diving dolphins routinely used interrupted patterns of swimming. This was especially apparent for deeper dives (Fig. 5). The initial descent period was characterized by constant dorso-ventral stroking. For dives to 210 m, the dolphins swam steadily for more than 90 % of the time during this initial period. In contrast, the final ascent often included periods of active stroking followed by gliding phases; 75 % of the final ascent period of 210 m dives was spent gliding. Mean stroke frequency was 69.3±1.8 strokes min^{-1} (N=17) during constant stroke periods for both the ascent and descent intervals.

Discussion

The effects of exercise on aerobic diving capacity in dolphins

The physiological responses of an actively diving mammal must account for the effects of apnea superimposed on swimming exercise (Castellini et al., 1985). While one response promotes the conservation of oxygen stores, the other simultaneously requires their utilization. Data from the present study in combination with previous work on swimming dolphins (Williams et al., 1993a) enable us to place the physiological responses attributable to apnea, exercise and the combination of both when diving within the physiological scope of the animals. On the basis of these findings, we can then examine the effect of these responses on the capacity of the animal to maintain aerobic metabolism during submergence.

The duration of submergence rather than the level of exercise *per se* appears to dictate many of the cardiovascular and respiratory responses of diving bottlenose dolphins. As reported for Weddell, harbor, grey and elephant seals (for a review, see Butler and Jones, 1997) and California sea lions (Ponganis et al., 1997), final bradycardia at depth is lower for longer dives or sedentary breath-holds by dolphins than for dives to shallower depths (Fig. 3). The bradycardia profile for actively diving dolphins was similar to that presented by Elsner et al. (1966) for trained submergence by bottlenose dolphins in an oceanarium pool. The previous study involved sedentary dolphins stationing at 2 m, while the present study used active dolphins performing dives up to 210 m (Fig. 3). Similarities in the level of bradycardia despite differences in activity for the study animals suggest an overriding influence of the dive response on exercise responses. This override feature appears to be most developed in highly adapted marine mammals. Other aquatic vertebrates, including many species of diving birds (Butler and Jones, 1997) and the hippopotamus (Elsner, 1966), show increased variability in heart rate when exercise is superimposed on apnea during submergence. Curiously, immature California sea lions maintain a response intermediate between that of dolphins and that of the hippopotamus. The level of bradycardia developed by immature sea lions was consistently less intense during trained dives than during submerged swimming at comparable periods of apnea (Ponganis et al., 1997). The young age of the sea lions and the nature of trained dives may have contributed to these results.

For diving marine mammals, the physiological effects of exercise and apnea on cardiovascular and respiratory systems may be manifest primarily during the post-dive recovery period. Several studies on pinnipeds (Thompson and Fedak, 1993; Andrews et al., 1997) have suggested that comparatively high physiological rates during the post-dive period benefit the marine mammal by reducing the requisite recovery time and shortening the inter-dive surface interval. Both the heart rate and respiratory rate of the dolphins during the initial post-dive recovery period were equivalent to or exceeded values reported for transit swimming (Figs 3, 4). The rates were positively correlated with dive depth and, hence, with the duration of submergence. Respiratory rate during recovery from the deepest dives reached the maximum level reported for dolphins

(Williams et al., 1993a). Similar patterns for respiratory rate have been reported for swimming and diving white whales. Like bottlenose dolphins, white whales demonstrate an increase in respiratory rate during recovery that correlates with the duration of trained dives (Shaffer et al., 1997).

Changes in blood parameters, most notably plasma lactate concentration (Fig. 2), of bottlenose dolphins also reflect the additive effects of exercise and apnea. As might be expected, sedentary breath-holding resulted in immediate changes in blood gas levels followed by a gradual change in lactate concentration. A linear decrease in blood P_{O_2} and increase in P_{CO_2} occurred during the first 225 s of apnea by sedentary dolphins (Fig. 1). The accompanying changes in lactate concentration during this period were insignificant (at $P<0.05$), increasing by less than 40 % over resting values (Fig. 2). Exercise, whether in the form of transit swimming on the water surface, stationary pushing against a force transducer or open-ocean diving, incurred higher lactate loads than sedentary breath-holding. The gradual rise in lactate level with the addition of exercise is comparable in scale with that of running terrestrial mammals (Seeherman et al., 1981) and is apparent in active dolphins regardless of continuous or interrupted access to air. Blood lactate level averaged $2.9\pm0.4\,\mathrm{mmol\,l^{-1}}$ for dolphins swimming at $2.1\,\mathrm{m\,s^{-1}}$; this increased to $3.4\pm0.0\,\mathrm{mmol\,l^{-1}}$ at $2.9\,\mathrm{m\,s^{-1}}$ (Williams et al., 1993a). Post-dive lactate concentration remained below these levels until the period of submergence exceeded 220 s (Fig. 2). Because diving dolphins tend to move over a slower range of speeds than transit-swimming animals (Table 1), the comparatively higher lactate concentrations undoubtedly result from the cumulative effects of apnea and exercise. Interestingly, the highest post-dive plasma lactate concentration, $6.4\,\mathrm{mmol\,l^{-1}}$, was nearly six times resting values but only 57 % of the maximum reported for bottlenose dolphins exercising against a force transducer. Dolphins in the exercise study were unable to sustain work at this level even though access to air was uninterrupted.

The onset of post-dive lactate accumulation may be predicted from the aerobic dive limit (ADL) of the animal (Kooyman and Ponganis, 1998). Defined as the maximum breath-hold that can be supported by available oxygen reserves without a post-dive rise in plasma lactate level (Kooyman, 1985), the ADL is calculated by dividing the on-board oxygen reserves by metabolic rate. Previous calculations for an adult bottlenose dolphin indicate a total oxygen reserve of $33\text{–}36\,\mathrm{ml\,O_2\,kg^{-1}}$ body mass (Williams et al., 1993b; Kooyman and Ponganis, 1998). Using the calculations of Kooyman (1989), the predicted ADL based on total oxygen stores ($33\,\mathrm{ml\,O_2\,kg^{-1}}$) and the resting metabolic rate ($7.39\,\mathrm{ml\,O_2\,kg^{-1}\,min^{-1}}$) of sedentary dolphins is 268 s (4.5 min). This decreases to 80 s (1.3 min) for a dolphin swimming continuously at $2.9\,\mathrm{m\,s^{-1}}$.

The predicted values for ADL correspond well with the changes in blood gas levels and lactate concentration measured in sedentary breath-holding dolphins. Breakpoints in blood P_{O_2} and P_{CO_2} occurred following 225 s of sedentary breath-holding (Fig. 1). Lactate concentration remained within 27 % of resting values until the duration of apnea exceeded 270 s (Fig. 2). It is important to note that the ADL does not necessarily correlate with or imply the depletion of all oxygen reserves in a diving animal (Kooyman and Ponganis, 1998). The changes in blood gas levels in the mixed venous samples obtained in the present study indicate a breakpoint near the ADL but not a depletion in this oxygen reserve.

The correlation between the predicted ADL and the onset of lactate accumulation is less clear for actively diving dolphins. When the metabolic costs of exercise are added to the calculations, the predicted aerobic limit is reduced. Using measured ascent and descent rates and bottom times (Table 1) and the corresponding metabolic rates of swimming and resting dolphins (Williams et al., 1992), the predicted aerobic dive limit is 181 s (3.0 min) for dolphins performing a 210 m dive. Changes in blood lactate concentration for open-ocean diving dolphins indicate a breakpoint at 222 s, approximately 23 % longer than predicted (Fig. 2). Average duration for 210 m dives was 247 s for the dolphins in the present study; this was 36 % longer than the predicted ADL. Differences between the predicted and measured ADL (based on changes in blood lactate concentration) reflect the lack of information regarding diving metabolic rates of free-ranging dolphins. Furthermore, it is difficult to estimate metabolic rates without knowing the behavior or activity level of the submerged dolphin. Forward velocity may be maintained by constant stroking or by interrupted patterns of swimming that incorporate prolonged glide sequences (Fig. 5). The energetic consequence of each on oxygen stores may be quite different.

Strategies for reducing locomotor costs during diving

Theoretically, the complex balance between exercise and diving responses will contribute to energetic savings during diving through the judicious use of oxygen stores. The strategy for many species of marine mammal appears to be adherence to a range of dive durations that is supported by aerobic metabolic pathways (Dolphin, 1987; Feldkamp et al., 1989; Kooyman, 1989; Kooyman et al., 1983; Ponganis et al., 1993; Martin et al., 1994; Shaffer et al., 1997). Indeed, the majority of dives (over 90 % for some pinnipeds) fall within this 'aerobic dive limit'. Diving profiles of free-ranging, small cetaceans are well within the aerobic limits predicted in the present study. Coastal populations of wild *Tursiops* sp. in 7 m depths off Florida (Shane, 1990) and 39 m depths near Golfo San Jose, Argentina (Würsig, 1978; Würsig and Würsig, 1979), demonstrate mean dive times of less than 25 s. A male juvenile bottlenose dolphin off the coast of Pembrokeshire, Wales, had a mean dive duration of 55.3 s and a maximum dive duration of 150 s (Lockyer and Morris, 1987). Recent studies using satellite and dive recorder technologies on dolphins similar in size to *Tursiops* provide additional information on the range of diving behaviors of small cetaceans. A 127 kg Atlantic spotted dolphin (*Stenella frontalis*) diving in water 33 m deep along the Gulf coast of Texas maintained 93 % of its dives to less than 120 s (Davis et al., 1996). The longest dives by this animal ranged from 300 to 360 s. In a study using time/depth recorders, the diving behavior of spotted dolphins (*Stenella attenuata*) was recorded in the Eastern Pacific Ocean. Average dive duration for this species was 120 s, with 90 % of dives lasting less than 210 s (M. Scott, personal communication; Scott et al., 1993).

To perform the 210 m dive in this study, bottlenose dolphins remained submerged for over 243 s (Table 1). Calculations based on swimming metabolic rates matched to ascent and descent rates indicate that the oxygen stores of the dolphin would have been exceeded by 28 %. The apparent energetic shortfall was not compensated for by a large anaerobic response when compared with maximum exercise levels (Fig. 2). Rather, the diving animals changed their mode of swimming. Whereas transit-swimming dolphins moving near the water surface maintain constant stroking, diving bottlenose dolphins incorporated prolonged glide periods and interrupted patterns of propulsion (Fig. 5; see also Skrovan et al., 1999). Energetic savings associated with burst-and-glide activity (Weihs, 1974; Blake, 1983b) or simply the absence of muscular effort during extended glides probably contributed to the observed prolongation of dive duration.

Physical factors associated with diving at depth may also play a greater role in conserving oxygen stores of dolphins than previously appreciated. Ridgway et al. (1969) found that bottlenose dolphins swimming horizontally at a depth of only 20 m showed lower pulmonary oxygen reserves, and therefore greater metabolic demands, than the same animals diving vertically to 200 m. Lung compression (Ridgway et al., 1969) and modifications in swimming mode resulting from changes in buoyant forces (Skrovan et al., 1999) during deep vertical dives may have promoted the savings. Although we were unable to observe the dolphins in the present study throughout the entire dive, preliminary evidence suggests that changes in buoyancy and swimming mode during ascent and descent provide an important opportunity for saving energy at depth (Fig. 5). Similarly, it is becoming increasingly evident that changes in swimming mode, like changes in gait by running vertebrates, are an important characteristic for deep-diving mammals including elephant seals (Williams et al., 1996; Webb et al., 1998) and Weddell seals (T. M. Williams, unpublished data). This is discussed further for diving dolphins by Skrovan et al. (1999).

In summary, the results of this study indicate a complex relationship between the physiological responses to exercise and diving in bottlenose dolphins. Regardless of depth, apnea results in the initiation of bradycardia and a gradual transition to anaerobic pathways as oxygen stores are reduced. The addition of exercise results in a quicker transition, as shown by comparatively higher blood lactate concentrations. Similarly, Castellini (1988), using metabolic turnover techniques, concluded that even short periods of apnea in seals result in a metabolic transition that distinguishes diving from exercise responses. As oxygen stores theoretically become limited during prolonged dives, dolphins incorporate prolonged periods of gliding and interrupted patterns of swimming. These locomotor modes take advantage of changes in pressure and buoyancy with depth and could provide unique opportunities for conserving limited oxygen stores during submergence in these cetaceans. Consequently, calculations based on the metabolic rate of dolphins actively swimming during ascents and descents will overestimate the actual energetic cost of the dive and underestimate the aerobic dive limit.

This series of papers on the diving physiology of dolphins was inspired by the work of Gerald L. Kooyman; they are dedicated to him in celebration of his remarkable research career and influence on all comparative physiologists. This study was supported by an ASSEE-ONT fellowship to T.M.W. and includes procedures and results from AMBS project SR02301. Additional research and analysis were supported by ONR grant N00014-95-1-1023 to T.M.W. The authors also thank S. Shippee and N. Chun for their invaluable assistance in sample collection at sea, and two anonymous reviewers and D. Noren, S. Noren, R. Davis and S. Kohin for helpful comments on drafts of the manuscript. All experimental procedures were evaluated and approved according to animal welfare regulations specified under NIH guidelines.

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THE DIVING PHYSIOLOGY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

II. BIOMECHANICS AND CHANGES IN BUOYANCY AT DEPTH

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Summary

During diving, marine mammals must balance the conservation of limited oxygen reserves with the metabolic costs of swimming exercise. As a result, energetically efficient modes of locomotion provide an advantage during periods of submergence and will presumably increase in importance as the animals perform progressively longer dives. To determine the effect of a limited oxygen supply on locomotor performance, we compared the kinematics and behavior of swimming and diving bottlenose dolphins. Adult bottlenose dolphins (*Tursiops truncatus*) were trained to swim horizontally near the water surface or submerged at 5 m and to dive to depths ranging from 12 to 112 m. Swimming kinematics (preferred swimming mode, stroke frequency and duration of glides) were monitored using submersible video cameras (Sony Hi-8) held by SCUBA divers or attached to a pack on the dorsal fin of the animal. Drag and buoyant forces were calculated from patterns of deceleration for horizontally swimming and vertically diving animals. The results showed that dolphins used a variety of swimming gaits that correlated with acceleration. The percentage of time spent gliding during the descent phase of dives increased with depth. Glide distances ranged from 7.1±1.9 m for 16 m dives to 43.6±7.0 m (means ± S.E.M.) for 100 m dives. These gliding patterns were attributed to changes in buoyancy associated with lung compression at depth. By incorporating prolonged glide periods, the bottlenose dolphin realized a theoretical 10–21 % energetic savings in the cost of a 100 m dive in comparison with dives based on neutral buoyancy models. Thus, modifying locomotor patterns to account for physical changes with depth appears to be one mechanism that enables diving mammals with limited oxygen stores to extend the duration of a dive.

Key words: dolphin, *Tursiops truncatus*, diving, biomechanics, buoyancy.

Introduction

Animals demonstrate a wide variety of mechanical, morphological and behavioral adaptations that promote locomotor efficiency and subsequently reduce the overall cost of activity. Terrestrial animals systematically change gaits, moving from walk to trot to gallop as speed increases (Heglund et al., 1974; Taylor, 1978; Hoyt and Taylor, 1981; Magana et al., 1997). During walking, these animals conserve energy by alternately storing and releasing gravitational potential energy as they rotate over a stiffened limb. With the change to a gallop, bound or hop, elastic elements in the limbs and spine may be used to store and recover energy as the speed of a terrestrial animal increases (Taylor, 1978; Williams, 1983).

Similarly, aquatic vertebrates use a variety of strategies to reduce the cost of locomotion. Burst-and-glide swimming and schooling, observed in many species of fish, promote energy conservation (Fish et al., 1991). The low drag associated with gliding periods during interrupted forms of swimming appears to compensate for the increased effort of re-acceleration during burst phases (Blake, 1983). Schooling behavior also reduces the energetic cost for individuals moving in groups by decreasing the relative drag encountered by the trailing swimmers (Breder, 1965; Belyayev and Zuyev, 1969; Weihs, 1973; Abrahams and Colgan, 1985).

Locomotor efficiency is especially important for aquatic mammals during diving. When submerged, marine mammals must balance the energetic demands of exercise with the conservation of a limited oxygen store (Castellini, 1985; Castellini et al., 1985). High locomotor costs will presumably lead to the termination of a dive as oxygen reserves are quickly depleted. Conversely, locomotor efficiency may be manifest as an increase in time available at depth for locating and catching prey or for predator avoidance (Williams, 1996).

Most studies addressing locomotor performance in marine mammals have focused on transit-swimming animals moving near the water surface (Fish, 1992). For example, the routine speeds (Lang and Norris, 1966; Lang, 1974; Würsig and Würsig, 1979; Williams et al., 1992), boundary flow characteristics (Rohr et al., 1998) and burst performances (Hui, 1987) of bottlenose dolphins have been reported. In comparison, there is little information concerning the underwater performance capabilities and limitations of these animals. In view of this, the present study examined the behavior and biomechanics of diving bottlenose dolphins (*Tursiops truncatus*) and the effect of a limited oxygen supply on underwater performance. Factors contributing to locomotor efficiency during submergence were investigated. To assess the relationships between swimming mode, stroke mechanics and dive depth, we videotaped dolphins during (1) horizontal swimming near the water surface, (2) horizontal swimming at depth, and (3) vertical diving to depths ranging from 12 to 112 m. Digital analyses of the video sequences were used to define locomotor modes and their pattern of use, glide duration and rates of acceleration and deceleration. These data, in combination with information from time/depth and velocity recorders, allowed changes in drag and buoyancy due to depth to be determined. The results of this study indicate that dolphins exploit changes in buoyancy associated with pressure changes at depth. By incorporating prolonged glide periods during descent, dolphins can reduce the period of active stroking and related energetic costs. Thus, glide performance by dolphins provides one important mechanism for conserving limited oxygen stores during submergence.

Materials and methods

Animals

Six trained Atlantic bottlenose dolphins (*Tursiops truncatus*) were used in this study (Table 1). All animals were housed in net pens (>15 m×15 m×4 m deep) connected to the open ocean. The dolphins were fed a diet of capelin and herring supplemented with multivitamins (Sea Tabs™, vitamin C, B-12 and B complex). Five of the animals were housed at the Dolphin Experience (Grand Bahama Island, Bahamas). Two adult male dolphins (B1, B2) and one adult female (B3) were used during uninstrumented dives to 12–14 m and for horizontal swims on the water surface and while submerged. A second female (B4) and an immature male (B5) were also used for surface swimming tests. Deep dives and horizontal submerged swims were performed by an adult male dolphin (S6) wearing an instrument package. This animal was housed at the U.S. Navy SPAWAR Systems Center (San Diego, California, USA).

Experimental design

The swimming mechanics and behavior of dolphins were examined under four conditions: (1) steady-state horizontal swimming near the water surface, (2) horizontal swimming at depths of 5–14 m, (3) shallow dives to 12 m without instrumentation on the dolphins, and (4) deep dives ranging from 16 to 112 m with the animal wearing an instrumentation package. Horizontal swimming, both near the surface and at depth, was used to evaluate the swimming mode of dolphins in the absence of changes in buoyancy. Deep dives of 16–112 m allowed a comparison of locomotor behaviors as buoyancy and demands on oxygen reserves changed with the depth and duration of the dive. Swimming and gliding performance of dolphins with and without instrumentation were also compared to determine the potential effects of the instrument package on the locomotor behavior and hydrodynamic drag of the animals.

Table 1. *Age and morphological dimensions of the bottlenose dolphins used in this study*

Animal	Age (years)	Length (cm)	Fluke span (cm)	Mass (kg)	Location
B1	13	249	64	236	Bahamas
B2	13	254	72	227	Bahamas
B3	13	237	68	173	Bahamas
B4	13	233	61	177	Bahamas
B5	2	188	N/A	82	Bahamas
S6	16	236	66	177	San Diego

Age was estimated from body length and duration in captivity.

Body length is the straight-line distance from the tip of the rostrum to the fluke notch.

N/A, not applicable.

Horizontal swimming

The kinematics of bottlenose dolphins swimming near the water surface was recorded using a hand-held video camera (Sony Hi-8, model CCD TR400). Dolphins were videotaped while swimming alongside a 17 foot Boston Whaler traveling at either 1.5 or 3.7 m s^{-1}. Boat speed was controlled by maintaining the outboard motor at constant revs min^{-1} with the same motor trim for all runs. Speed associated with each revs min^{-1} was determined by videotaping the boat's passage past fixed points a measured distance apart. Video sequences of the fixed points were digitized, and speed was determined using a motion-analysis system (Peak Performance Technologies, Inc.; Englewood, CO, USA). Trainers maintained the position of the dolphins abeam of the boat outside the stern and bow wakes. Analyses were limited to video segments in which the dolphins remained clear of interfering wakes and were stationary relative to the moving boat.

Horizontal swimming was also examined for submerged dolphins moving between two trainers at a depth of 14 m or between stationary targets at approximately 5 m depth. During the 14 m trials, movements of the dolphins were recorded by a SCUBA diver with a hand-held video camera in a submersible housing (Stingray, Inc.). The camera was held in a stationary position perpendicular to the swimming path of the animals. Progress across the field of view was converted to speed (m s^{-1}) using the motion-analysis system described above.

Images were digitized and calibrated against the measured length of the dolphin. To account for extraneous movements of the camera, a fixed point on the sea floor within the field of view was digitized using Peak Performance software (Englewood, CO, USA). Movement vectors of the fixed point were then subtracted from movement vectors of the dolphin. In addition to these trials, fluke movements of a dolphin swimming horizontally at approximately 5 m depth were recorded for an animal wearing a submersible video/instrument package (described below). Horizontal swim paths at depth ranged from 10 to 100 m in length.

Shallow dives

Straight-line dives to less than 16 m in depth were recorded in the Bahamas by a SCUBA diver using a hand-held video camera in a submersible housing (described above). On each experimental day, two dolphins followed a motor boat to an open ocean site 1 mile (1.61 km) offshore. Sites ranged from 12 to 16 m in depth with a sand bottom. Dolphins were trained to dive between the boat and a trainer stationed at depth. The animals chose their rates of ascent and descent, surface interval between dives and bottom time. Each session was recorded by a diver positioned perpendicular to the movements of the dolphins and as far back as visibility allowed. Depending on the distance from the subject, the field of view for the camera was 7–14 m. A field of view of 14 m allowed the entire ascent and descent of the dolphins to be monitored without panning the camera. When necessitated by surge, a monopod was used to stabilize the camera. To control for inadvertent camera movement, a stationary reference point was digitized, and its movement vector was subtracted from the dolphin's track. Measurements of fluke movement and velocities were not sensitive to camera range because each video sequence was calibrated against the measured length of the dolphin.

Deep dives

Fluke movements during deep (16–112 m) diving were recorded by a submersible video camera worn by the dolphin. A saddle platform containing the camera and instrumentation was custom-fitted to the dorsal fin of one dolphin, S6. The dolphin was trained for 6 weeks prior to the experiments to swim and dive while wearing the instrument package. This on-board system enabled us to examine the fluke movements of the dolphins at depths exceeding 100 m, which were outside the range of SCUBA divers.

The instrument package included a time/depth recorder, velocity meter, camera head (See-snake) surrounded by blue light-emitting diodes and video recorder. The camera head was directed backwards to record the stroke activity of the dolphin's fluke. Video sequences and dive variables were synchronized using custom-designed software (Pisces Design; San Diego, CA, USA). The instrument package and platform were neutrally buoyant and constructed of non-compressible materials to maintain neutrality at depth. The mass of the package was 14 kg, representing 8 % of the dolphin's mass. Because the package was neutrally buoyant, there was no additional weight for the dolphin to bear. However, its mass affected the acceleration of the dolphin. Details of the camera and instrument package are described by Davis et al. (1999).

The stall speed and accuracy of the velocity meter, as well as the accuracy of the time/depth recorder, were determined prior to deployment. The minimum recording (stall) speed of the velocity meter was measured by towing the instrument package attached to a fusiform shape through an annular water trough (Scripps Institute of Oceanography, La Jolla, CA, USA). In addition, the velocity meter was self-calibrated on the diving dolphin by plotting the velocity of the animal against the rate of depth change (S. Blackwell, personal communication). The latter method provides accurate calibration of the velocity meter if any portion of a dive is near vertical. Observations from the surface and video recordings indicate that this condition was met in the present study. The depth sensor was calibrated before and after the experimental period. The accuracy of the depth sensor was tested on a pressure station at 0–1500 psi (0–10.4 MPa) and was found to be linear over the test range (r^2=0.99) with a mean standard deviation of ±0.2 %. Depth and velocity were recorded at 1 s intervals throughout the dives.

Ten dives to 16 m were conducted inside San Diego Bay, CA, USA. During these trials, the dolphin followed a boat (Boston Whaler, 21 foot) to the dive site, where the instrument package was placed on the dolphin and secured using a strap. An acoustic pinger attached to a video camera was lowered to 16 m. The camera was cabled to a monitor on the boat and used to confirm the animal's arrival at depth. Following a signal from the trainer, the dolphin submerged to the pinger. On arrival, the acoustic signal was turned off and the animal returned immediately to the boat. A rest period of at least 1 min was provided between dives. The mean rest period was 46±23 s before the dolphin voluntarily began diving.

Eighteen dives of 50–112 m were conducted in the open ocean approximately 5 miles (8.1 km) off the coast of San Diego, CA, USA. To avoid fatigue during these deep diving tests, the dolphin was transported by boat to the dive site, where it was immediately returned to the water. The instrument package was placed on the dolphin, and the acoustic pinger was lowered to the test depth (50 or 100 m). Testing procedures were as described for 16 m dives. Recovery periods averaged 2.5 min between dives, during which the respiratory rate of the animal was monitored. Respiratory rate was determined by counting the number of breaths taken during the first minute immediately following the dive (Williams et al., 1999).

Analysis

The swimming mode and kinematics of uninstrumented dolphins were determined from video sequences from the hand-held camera using a motion-analysis system (Peak Performance Technologies, Inc.; Englewood, CO, USA). Each swimming or diving segment was converted to digital format. Anatomical points of interest (for details, see Fig. 1A) were manually digitized for 1–60 images per second of video recording. The acceleration, deceleration, angular acceleration and speed of each point were then computed. In addition, stroke amplitude and the distance traveled by the dolphins while stroking or gliding were assessed for each video sequence. Changes in the amplitude (as a proportion of total body length) of the anatomical points were calibrated against the measured length of each dolphin.

Video images from the instrument package worn by the dolphin on deep dives were copied onto VHS tapes with data overlay from the time/depth recorder and velocity meter. The annotated video recording was analyzed 'frame by frame' for patterns in swimming mode and type of stroke. Strokes were categorized as large, medium, small or gliding according to the arc swept by the fluke. Stroke type was correlated to changes in depth, speed and acceleration of the dolphin.

Drag and buoyant forces were determined from videotaped sequences of horizontally swimming or vertically diving dolphins, respectively. Total body drag was calculated by multiplying the measured rate of deceleration of horizontally gliding dolphins by the total mass decelerated. Deceleration was determined from the change in speed at 1 s intervals and averaged over the glide period. The mass of dolphin S6 was 177 kg, and the mass of the instrument package was 14 kg. Because accelerating a body within a fluid also involves accelerating the surrounding fluid (Daniel, 1984; Lovvorn et al., 1991; Vogel, 1981), we accounted for the mass of the entrained water moving with the dolphin. This is equivalent to the mass of water displaced by the animal multiplied by the coefficient of added mass (0.06 for a prolate spheroid of fineness ratio 5.0; Vogel, 1981). On the basis of this calculation, the mass of the entrained water was 11 kg, and the total mass of the instrumented animal moving through the water was 202 kg. It is likely that the coefficient of added mass used in these calculations is conservative for a dolphin-shaped body and that the actual added mass may be greater because of water entrained by body contours or fins. Calculations based on a less-streamlined shape (i.e. a fineness ratio of 4.0) result in only a 2.1 % increase in the predicted total mass of the instrumented animal. Such a difference would not significantly alter our calculations for body drag and buoyant force.

Buoyancy in diving dolphins was calculated from the differences in deceleration between vertical and horizontal glides. The changes in buoyancy were ascribed to changes in volume with depth due to the compression of air spaces by water pressure. For dolphins, the lungs represent an important, compressible air space. Air in the lungs imparts a buoyant force equal to the amount of water displaced according to Archimedes' principle (Giancoli, 1984). During diving, pressure increases by 1 atm (98.1 kPa) for every 10 m increase in depth (Heine, 1995). Because volume varies inversely with pressure, the lung volume of the dolphins will decrease with depth. On the basis of these principles, the change in air volume of the lungs is described by:

$$V_D = V_S/(1 + 0.1h)\,, \qquad (1)$$

where V_D is air volume in liters at depth, V_S is the air volume in liters at the surface, and h is depth in meters. The buoyant force at any depth can be determined for the dolphin from lung volume added to the buoyant force of its body. The resulting equation is:

$$B_D = V_D g + B_B\,, \qquad (2)$$

where B_D is the buoyant force in newtons at depth, V_D is the air volume in liters at depth from equation 1, g represents the acceleration due to gravity (9.8 m s^{-2}) and B_B is buoyancy in newtons of the dolphin's body without air (−33.2 N for dolphin S6; see equation 7). Note that the air volume in liters is equivalent to the mass of the displaced water in kilograms. During vertical glide sequences, upward buoyant forces oppose the downward pull of gravity. The resultant force will hereafter be referred to as a positive buoyant force when the net force is upwards and as a negative buoyant force when the net force is downwards.

Effects of instrumentation on dolphin performance

Previous studies indicate that the addition of recording instruments may alter the performance of an aquatic animal by increasing drag and by adding inertial mass (Wilson et al., 1986; Boyd et al., 1997). The total frontal area of the instrument package in the present study represented approximately 22 % of the dolphin's frontal area. The instruments were evenly divided between each side of the dolphin, with the front end of the instruments being tapered to minimize drag. We determined the changes in total body drag of the dolphins due to the instrument package by comparing horizontal glide deceleration for instrumented and uninstrumented animals. Behavioral and mechanical effects of instrument drag were also assessed by comparing the stroke type, stroke frequency and speed of instrumented and uninstrumented dolphins. Data for uninstrumented dolphins were obtained from digital analysis of video recordings taken by a SCUBA diver. For the instrumented dolphin, data were obtained from video recordings as well as from velocity and depth recorders in the instrument package.

Statistics

Linear and curvilinear regressions were determined from least-squares methods using Sigma Plot (Jandel Scientific, 1995). Sigma Stat software (Jandel Scientific, 1995) and Zar (1974) were used for *t*-tests of paired data. Sums-of-squares analyses for curves were calculated using SuperAnova software. Values for significance were set at $P<0.05$. Means are reported ±1 S.E.M.

Results

Swimming gaits of bottlenose dolphins

Similar to previous reports (Videler and Kamermans, 1985; Fish and Hui, 1991), we found that the entire body of the dolphin oscillates as it swims. An undulatory wave progresses behind the dorsal fin down the peduncle to the fluke hinge and finally to the fluke tip (Fig. 1). The dorsal fin moves out of phase with the rostrum and fluke. Maximum upward excursion

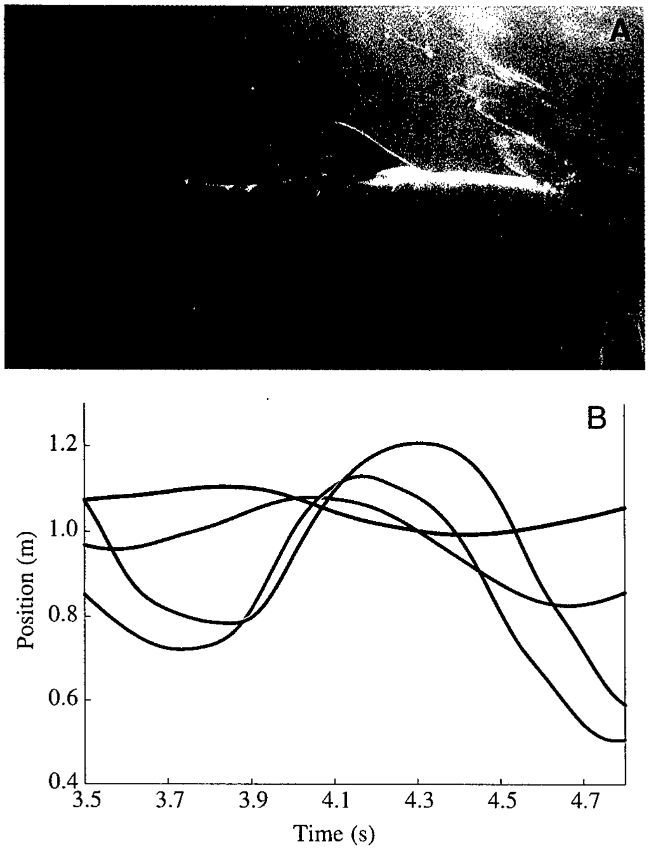

Fig. 1. Video image (A) and range of movement (B) of four anatomical sites during a single stroke for a bottlenose dolphin swimming horizontally next to a boat at 1.5 m s^{-1}. Colored squares in the picture correspond to the line colors illustrating the movements for each site. Note that the dorsal fin (dark blue) reaches its maximum excursion first, followed sequentially by the peduncle (red), the fluke hinge (green) and finally the fluke tip (pink).

of the fluke tip occurs as the dorsal fin is at the bottom of its cycle; the reverse occurs on the downstroke. Each anatomical site differed in range of movement. The amplitude and frequency of these movements were dependent on the speed and power requirements of the animal (Table 2). Both the present study and that of Fish (1993) found no change in fluke amplitude during steady swimming over the range of test speeds. Three different patterns or gaits were observed.

Large-amplitude strokes

The largest stroke amplitudes (representing 20–50 % of body length) occurred at the start of horizontal swims and at the beginning of the descent and ascent phases of dives. The amplitude of these strokes exceeded the range reported for steadily swimming dolphins in an aquarium pool at speeds ranging from 1.2 to 6.0 m s^{-1} (Fish, 1993). The use of this gait corresponded to the periods of greatest acceleration (3.5–4.7 m s^{-2}). The amplitudes for all body segments were larger than those observed during steady swimming. The greatest change in amplitude occurred at the rostrum and was four times that of steady swimming. In comparison, the fluke and dorsal fin regions more than doubled their amplitude during periods of acceleration, while the mid-peduncle region showed the least change (Table 2).

As a result of the methodology, only the movements of the flukes could be recorded during deep dives or horizontal swims at depths exceeding 14 m. Large-amplitude strokes were used during the initial 1–2 s of horizontal swims and initial descents of dives. The period for large-amplitude stroking increased up to 5 s during the initial ascent from 50 and 100 m dives.

Medium-amplitude strokes

Medium-amplitude strokes (approximately 20 % of body length) occurred during steady-state swimming at 1.5–3.7 m s^{-1}. Motion of the head was reduced in comparison with that occurring in association with large-amplitude strokes. The arc of the rostrum covered only 5 % of body length during medium-amplitude stroking. Similarly, the dorsal fin showed comparatively smaller amplitude movements.

There was a significant (P=0.05) increase in the frequency of medium-amplitude strokes with speed during steady swimming over the range 0.6–3.7 m s^{-1} (Fig. 2A). Dolphins

Table 2. *Primary locomotor modes of swimming and diving bottlenose dolphins*

Gait	Use	Duration	Stroke frequency (Hz)	Amplitude (% body length) R:D:F
Large-amplitude	Acceleration	Brief (1–5 s)	>0.43×speed (1.5 to >3 Hz)	20:10:40 Declines rapidly as speed increases
Medium-amplitude	Cruising	Extended (1 s to >1 min)	0.43×speed (0.5–3 Hz)	5:5:20
Glide	Energy conservation	Dependent on dive depth (1–50 s)	0	0:0:0

Stroke frequency increased linearly with speed during steady swimming (see text). During periods of acceleration, stroke frequency was higher than indicated by this relationship.

Relative changes in stroke amplitudes are given for the rostrum (R), dorsal fin (D) and fluke (F) for each gait.

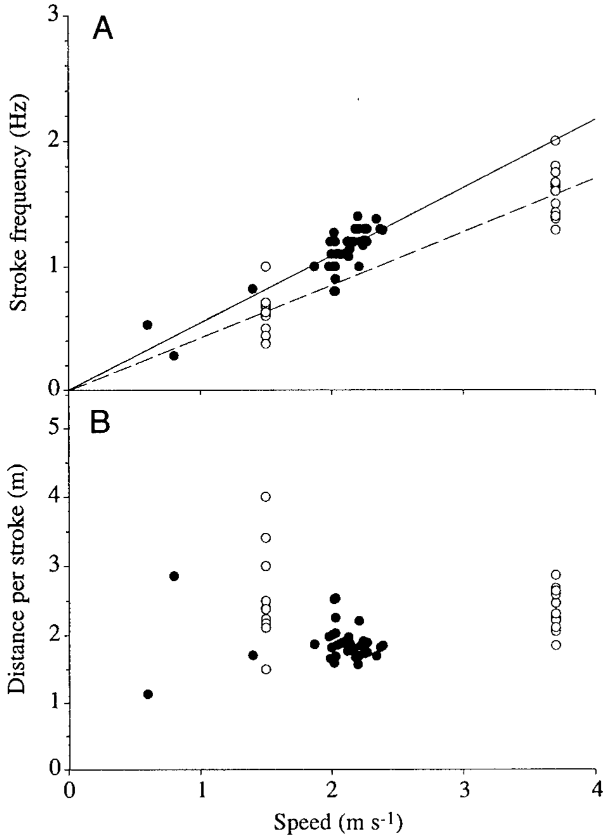

Fig. 2. Stroke frequency (A) and distance traveled per stroke (B) in relation to swimming speed for bottlenose dolphins. Data for instrumented (filled circles) and uninstrumented (open circles) dolphins are compared. Solid and dashed lines denote the least-squares linear regressions through the data points. Regressions for stroke frequency show a significant difference between the instrumented and uninstrumented animals ($P<0.05$). The distance moved per stroke was independent of speed in both groups of dolphins. Equations for the regression lines are given in the text.

with and without instrumentation showed linear increases in stroke frequency (f) with speed (v), but differed in the magnitude of the response. The regression for uninstrumented dolphins was:

$$f=0.43v \tag{3}$$

(N=30, r^2=0.90, $P<0.05$), where stroke frequency is in strokes s^{-1} (Hz) and speed is in m s^{-1}. The stroke frequency of the instrumented dolphin was approximately 27 % higher at comparable speeds to the uninstrumented dolphins and was described by the equation:

$$f=0.54v \tag{4}$$

(N=41, r^2=0.73, $P<0.05$). The distance traveled per stroke (Fig. 2B) did not change significantly with speed over the range tested for either the instrumented (r^2=0.008, N=41) or uninstrumented (r^2=0.01, N=30) dolphins. The mean distance per stroke was approximately 0.5 m (27 %) less for the instrumented dolphin than for uninstrumented dolphins swimming at comparable speeds.

Glides

Dolphins incorporated short (3–14 m) and long (>14 m) glide sequences during activity. Short glides occurred at the end of every ascent or descent, as the dolphin came to a stop or changed direction. Ascent glides ranged from 6 to 14 m in distance traveled (mean 9.3±2.5 m, N=28) and showed a mean deceleration of 0.07±0.12 m s^{-2} (N=10). Uninstrumented dolphins also demonstrated short periods of gliding associated with burst-and-glide propulsion during both horizontal submerged swimming and diving. These resulted in brief periods of deceleration before stroking resumed. The instrumented dolphin limited burst-and-glide propulsion to diving periods. We attribute the absence of burst-and-glide activity during horizontal swimming to the added drag of the instrument package. Long-distance gliding was an important component of the descent phase of dives for all dolphins. Glide distance varied with depth as described below.

Variations in gait

In addition to the three distinct gaits described above, dolphins utilized several variations of these patterns. Small-amplitude strokes (<20 % of body length) occurred intermittently as animals made the transition between active swimming and gliding. These smaller strokes also occurred between periods of medium-amplitude stroking. A variety of braking motions that included holding the fluke up, down or to either side were used by dolphins to decelerate.

Locomotor mode during swimming and diving

Horizontal swimming

Horizontal swimming by dolphins near the water surface or submerged at 5–16 m involved similar locomotor modes. For horizontal distances less than 15 m, the dolphins initially accelerated using large-amplitude strokes, followed by a period of decreasing stroke amplitude and finally passive gliding to the end point. The initial acceleration enabled the dolphins to reach speeds of 2.0–3.5 m s^{-1} in less than 2 s. Longer periods of steady-state swimming on the water surface at 1.5–3.7 m s^{-1} were accomplished by medium-amplitude stroking. Glide periods during steady-state swimming rarely exceeded 2 s.

Shallow dives

All shallow dives matched one of the following patterns with minor variation. Dives to 12 m by uninstrumented dolphins began with one or two large-amplitude strokes, resulting in a travel speed of 2.0 m s^{-1}. Starting at a depth of 4–6 m, the animals glided for approximately 5 m before braking or veering into a horizontal glide. Because of the short distance involved, the dolphins were able to glide to the surface after one or two medium-amplitude strokes at the start of the ascent. Dives to 16 m by the instrumented dolphin also began with a short period of active stroking followed by a short glide. The dolphin actively swam downwards for 9.0±1.9 m (N=10) before gliding the remaining 7.1±1.9 m (N=10). After braking, the dolphin used large-amplitude strokes to begin the ascent. Medium-amplitude strokes were used throughout the mid portion of the

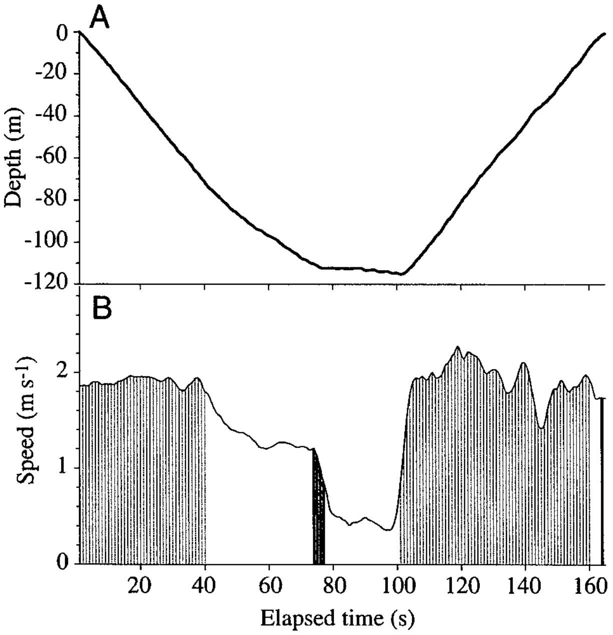

Fig. 3. Representative changes in depth (A) and speed and stroke pattern (B) in relation to dive time for an instrumented dolphin. Maximum dive depth was 112 m. Grey bars denote periods of stroking in which glide periods were less than 1 s in duration. Open areas show periods of continuous gliding or stationing. Black bars indicate braking at the end of the descent and ascent. Note the change in deceleration at 60 s midway through the gliding decent.

ascent. As the dolphins approached the surface, stroke amplitude decreased to zero, with the dolphin gliding the remaining 9.1±2.6 m (N=10).

Deep dives

The instrumented dolphin performed ten dives to depths of 50 m and eight dives to depths of 100–112 m. As observed for shallow dives, the dolphin used large-amplitude strokes to begin the descent, followed by medium-amplitude stroking. Intermittent stroking patterns incorporating short periods of gliding between active stroking often occurred during deep dives (Fig. 3). These periods of intermittent propulsion were characteristic for descents and ascents of deep dives but were not observed for shallow dives.

The percentage of time spent gliding during descent changed with depth for the diving dolphins. During 50 m dives, the dolphin glided for 30.3±2.8 % (N=10) of the descent. This increased significantly (at P<0.001) to 51.2±3.3 % (N=8) during the 100–112 m dives.

Glide distance for the 50 m dives, 12.3±3.6 m (N=10), was not significantly different (at P=0.21) from the average for 16 m dives. However, glide distance during the descent increased significantly (P=0.01) with dive depths greater than 50 m. The total length of the glide was 43.6±7.0 m (N=8) during 100–112 m dives (Fig. 4). Glides occurring during the ascent showed no significant changes with depth (P=0.27).

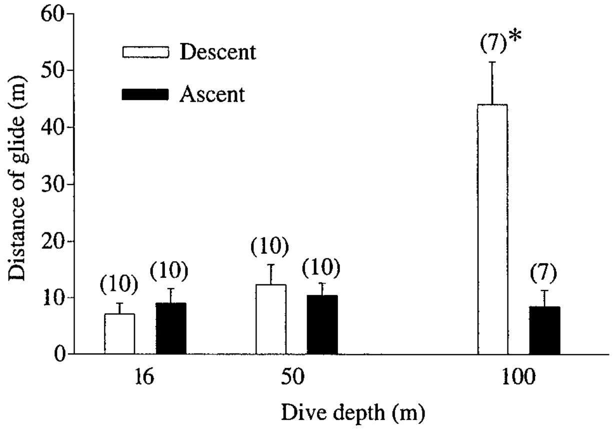

Fig. 4. Glide distance during descent (open columns) and ascent (filled columns) segments of dives in relation to depth for bottlenose dolphins. The height of the columns and lines shows the mean value +1 S.E.M. Numbers in parentheses indicate the total number of dives examined. An asterisk indicates a significant difference between the descent and ascent values for 100 m dives. Glide distances were not significantly different (at P<0.05) between ascent and descents for dives ranging from 16 to 50 m. In contrast, significant differences (at P<0.001) were found between glide distances for the descent and ascent segments of the 100 m dives.

The speed of the dolphins during diving was correlated with gliding or stroking periods. An example is shown in Fig. 3. During stroking on the descent of a 112 m dive, the speed of the dolphin was approximately 1.9 m s^{-1}. Cessation of stroking resulted in a period of deceleration that was followed by a constant speed of 1.2 m s^{-1} during the remainder of the descending glide. Speed during the ascent was more variable and corresponded with burst-and-glide activity (Fig. 3).

As with shallower dives, a braking motion occurred at the end of descent, followed by large-amplitude strokes at the beginning of ascent. Average glide distance to the surface was 10.4±2.2 m (N=10) on 50 m dives and 8.5±2.9 m (N=8) on 100–112 m dives.

Drag and buoyant forces

The drag of the dolphins increased significantly with speed and was comparatively higher for the instrumented dolphin (Fig. 5). The least-squares curvilinear regression for the instrumented dolphin was:

$$D = 1.78 + 8.93v^{2.99} \tag{5}$$

(r^2=0.64, P=0.220, N=6). The regression for uninstrumented dolphins was:

$$D = 4.15v^{2.00} \tag{6}$$

(r^2=0.65, P=0.097, N=5), where drag (D) is in newtons and speed (v) is in m s^{-1} for both equations.

For deep-diving dolphins, measured deceleration during gliding changed with depth because of changes in buoyant force. For example, the mean depth during prolonged (>2 s) descending glides was 67.5±23.0 m, with a glide speed of 1.5±0.3 m s^{-1} and a mean deceleration of 0.03±0.06 m s^{-2}

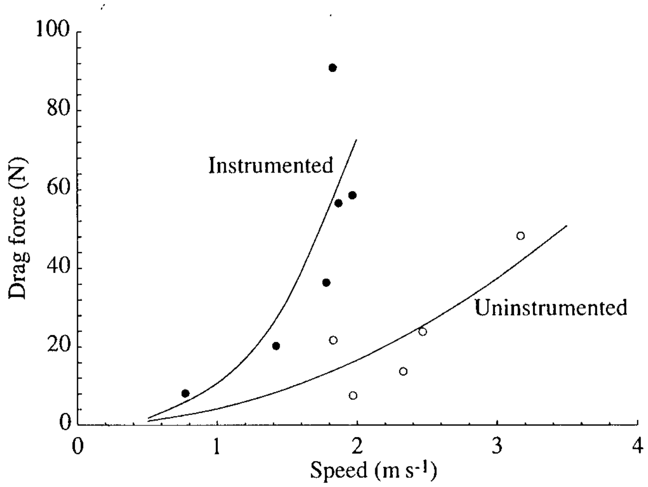

Fig. 5. Body drag in relation to horizontal glide speed for instrumented (filled circles) and uninstrumented (open circles) bottlenose dolphins. Solid lines denote the least-squares curvilinear relationships through the data points. All glide sequences took place at depths greater than three body diameters below the water surface to avoid surface wave effects. Speed represents the mean speed during each glide sequence. Equations for the relationships are given in the text.

(N=27 glide sequences). The decelerating force acting on vertically diving dolphins, calculated from the product of deceleration ($0.03\,\mathrm{m\,s^{-2}}$) and the mass of the instrumented dolphin including entrained water (202 kg), was 6.1 N. This compares with a drag of 31.8 N for gliding dolphins moving horizontally at the same speed (Fig. 5; equation 5). Presumably, the drag of the vertically diving dolphin was countered by a downward force of 25.7 N (31.8–25.7=6.1) (Table 3). Similar calculations for the ascent phase demonstrate the positive effect of buoyancy as a dolphin nears the water surface. The mean depth of gliding for ascent from instrumented dives was 5.5±2.2 m, with a mean speed of $1.6\pm0.2\,\mathrm{m\,s^{-1}}$ and deceleration of $0.07\pm0.12\,\mathrm{m\,s^{-2}}$ (N=10). The product of deceleration and mass is 14.1 N for the dolphins on a vertical ascent. In comparison, the calculated drag for horizontally gliding dolphins moving at $1.6\,\mathrm{m\,s^{-1}}$ is 38.4 N (equation 5). Thus, the final ascent drag was countered by an upward buoyant force of 24.3 N (38.4–24.3=14.1).

From these calculations, we find that the buoyant force acting on the diving dolphins in this study changed from +24.3 N near the water surface (5.5 m depth) to −25.7 N at a depth of 67.5 m, a difference of 50.0 N. This is equivalent to a change in water displacement of 5.1 l ($50.0\,\mathrm{N}/9.8\,\mathrm{m\,s^{-2}}$=5.1 kg or approximately 5.1 l of water). Such a change in displacement is reasonable since dolphins dive following inspiration and air compresses with depth. From equation 1, an initial lung volume of 8–10 l would be needed to achieve this magnitude of volume change in the diving dolphin, which is within the reported range for a 177 kg dolphin (Ridgway et al., 1969; Stahl, 1967).

Fig. 6 illustrates the changes in buoyant force of 8.5 l of air with depth for diving dolphins. This curve and the calculated buoyancy of the dolphin differed consistently by 33.2 N, and we assume that this was due to the weight of the dolphin's body. Thus, for the instrumented dolphin, diving with a lung volume of 8.5 l, equation 2 becomes:

$$B_{\mathrm{D}} = 83/(1 + 0.1h) - 33.2\,, \tag{7}$$

where B_{D} is the buoyant force in newtons at depth h in m, 83 N is the buoyant force of 8.5 l of air and −33.2 N is the buoyancy of the dolphin's body without air. The net force acting on the gliding dolphin can then be calculated from the difference between this buoyant force and total body drag (Fig. 5).

The above calculations are appropriate for gliding dolphins in which swimming motions are absent. To calculate the drag on swimming dolphins, we need to account for the additional drag due to locomotor movements. A conservative estimate of this active drag is three times that of the gliding animal (Lighthill, 1975, 1971; Webb, 1975, 1984; Williams and Kooyman, 1985; Fish, 1993).

Table 3. *Locomotor variables, total body drag and buoyant forces for a bottlenose dolphin during a 100 m dive*

	Deceleration ($\mathrm{m\,s^{-2}}$)	Speed ($\mathrm{m\,s^{-1}}$)	Net force (N)	Drag (N)	Buoyancy (N)	Depth (m)
Descent glide	0.03±0.06 (27)	1.5±0.3 (27)	6.1	31.8	−25.7	67.5
Ascent glide	0.07±0.12 (10)	1.6±0.2 (10)	−14.1	−38.4	24.3	5.5
Descent swimming		1.7±0.0	160.6	136.3	24.3	5.5
Ascent swimming		1.9±0.0	−213.6	−187.9	−25.7	67.5

Gliding and swimming during ascent and descent are compared.

Deceleration, speed and depth were measured for a dolphin wearing an instrument pack.

Net force, drag and buoyancy were calculated as described in the text. Drag calculations for swimming on ascent and descent include an active drag factor of 3 (Fish, 1993; Lighthill, 1971, 1975; Webb, 1975, 1984) to account for the additional drag associated with swimming movements.

All downward forces relative to the water surface are indicated by a negative sign.

Numbers in parentheses indicate N for the measured variables.

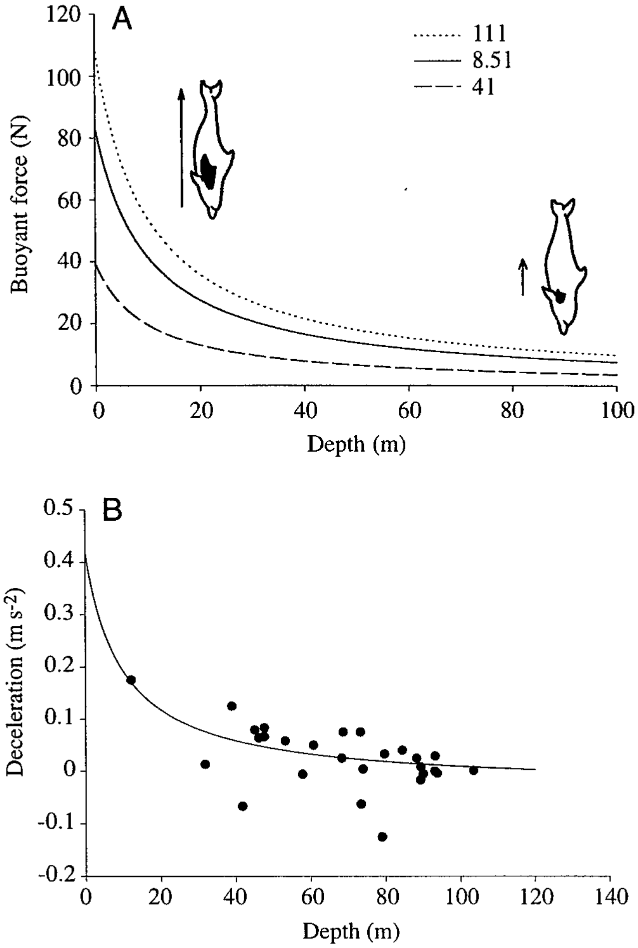

Fig. 6. Changes in the buoyant force of lung air (A) and deceleration (B) in relation to dive depth in bottlenose dolphins. Calculations for buoyant force are based on equations presented in the text and are compared for three different initial lung volumes. Note the rapid decline in buoyant force with depth as the water pressure progressively collapses the lungs. The decline in deceleration of gliding dolphins (B) determined from video analyses paralleled that calculated for buoyant force. Each point represents an individual glide sequence. The solid line in B is not a regression for the data, but rather the calculated deceleration based on buoyancy changes with depth (see text).

Effects of instrumentation

Average speeds during diving and horizontal swimming were 9–10 % lower for the instrumented dolphin than for uninstrumented dolphins. Drag was 3.3 times higher for the instrumented dolphin at the mean gliding speed of 1.47 m s^{-1} (Fig. 5). The elevated drag resulted in a 27 % reduction in distance achieved per stroke and a concomitant increase in stroke frequency (Fig. 2). Although stroke amplitude appeared to be higher for the instrumented dolphin, differences in measurement techniques for instrumented and uninstrumented animals prevented accurate comparisons. Because of the demonstrated effects of the instrumentation on drag and swimming mechanics, the glide distances reported here should be considered as conservative estimates of the true performance of uninstrumented dolphins performing deep dives.

Discussion

The importance of gait transitions during swimming and diving

Foraging aquatic mammals must divide their time between two important resources, oxygen located at the water surface and prey items located at depth (Dunstone and O'Connor, 1979). The swimming modes selected by mammals moving between these resources will affect their locomotor efficiency and, ultimately, the cost/benefit relationships for foraging. Previous studies with dolphins have shown that elevating swimming speeds during ascent and descent to decrease the duration of a dive leads to an extraordinarily rapid depletion of limited oxygen reserves (Williams et al., 1993). Travel too slowly, however, and time becomes limiting as basal metabolic demands exhaust the available oxygen (Williams et al., 1999).

Data from the present study demonstrate that bottlenose dolphins tailor their swimming patterns to diving depth, a strategy that leads to energetic efficiency (Figs 3, 4). As found for running animals (Heglund et al., 1974; Taylor, 1978; Hoyt and Taylor, 1981), changes in gait by swimming and diving dolphins were associated with specific tasks and speeds (Table 2; Fig. 3). Dolphins switched gaits primarily in conjunction with acceleration needs. During initial acceleration from rest, stroke frequencies and fluke amplitudes often exceeded those used during steady swimming. Large-amplitude movements of the head and back accompanied these large fluke motions. The tip of the rostrum showed an excursion of nearly 20 % of body length, while fluke amplitude exceeded 40 % of body length (Table 2). As the dolphin's speed increased, stroke amplitude gradually decreased to the values observed during steady-state swimming. These results are consistent with models that predict increased mechanical efficiency during low-speed swimming when thrust is produced by accelerating a large mass of fluid (per time) to a low velocity instead of accelerating a small mass to a high velocity (Alexander, 1977).

During diving, dolphins minimized the use of large-amplitude strokes and incorporated prolonged glide periods as speed and coincident drag increased. Large-amplitude strokes only occurred for brief (<5 s) periods during the initial descent and ascent. Except for these initial periods, diving dolphins relied on medium-amplitude strokes and, when possible, even smaller stroking movements. The smaller-amplitude strokes occurred during transitions between steady-state stroking and gliding, with stroke frequency remaining unchanged. These results are not surprising when the hydrodynamics are considered. High-amplitude movements are a departure from the streamlined shape of the dolphin and theoretically result in elevated levels of drag, especially as stroke amplitude is increased (Fish et al., 1988; Lighthill, 1971; Webb, 1975). An actively swimming animal may encounter a three- to fivefold increase in total body drag over gliding values as a result of elevated pressure drag (Fish et al., 1988), separation or thinning of the boundary layer (Lighthill, 1971) and increased drag from thrust production (Webb, 1975). The marked effect of even small adjustments in posture on drag and forward movement of the dolphin was observed when an animal used braking movements to reduce speed. Raising the fluke a distance equivalent to 10 % of body length resulted in an 11.5-fold increase in total body drag.

Although prolonged gliding allows diving dolphins to avoid active drag, it places a limit on maintaining propulsion. To circumvent this, dolphins and other swimmers often rely on a burst-and-glide style of swimming that incorporates short periods of stroking during prolonged glide sequences to maintain forward speed (Videler, 1981; Videler and Weihs, 1982; Weihs, 1974). Despite elevated drag associated with re-acceleration between glides, the calculated energetic cost for this interrupted mode of swimming is significantly lower than for continuous swimming (Blake, 1983).

Because dolphins produce power by oscillating their flukes (Lang and Daybell, 1963; Slijper, 1961; Videler and Kamermans, 1985), the mass of the fluke plus entrained water must be decelerated to a stop then re-accelerated in the opposite direction both at the top and bottom of each stroke. The alternate storage and release of elastic energy in conjunction with fluke movements could serve as a potential energy-conserving mechanism. Changes in the axial body of the swimming dolphin are qualitatively similar to those of galloping terrestrial mammals in which the trunk is used as a spring to store elastic energy (Taylor, 1978). Several spring-like tissues have been implicated as energy-saving mechanisms for swimming dolphins. Pabst (1990) described a crossed, helically wound, fiber array encasing the dolphin body. The fiber array, derived from ligaments, muscle tendons and blubber tissue, gains rigidity because of the tension it is under. This array may act as a spring, storing energy during part of the stroke cycle and recovering it during the remainder (Pabst, 1990). Although intriguing, such elastic storage mechanisms have yet to be tested in a freely swimming dolphin and warrant further investigation.

The swimming mechanics of dolphins share other features common to terrestrial animals and swimming humans. In terrestrial mammals, stride frequency increases linearly with speed during walking and trotting. As speed increases, many runners switch to a gallop in which speed is achieved by lengthening the stride rather than by increasing stride frequency (Heglund et al., 1974). Conversely, human swimmers decrease the distance per stroke (the aquatic equivalent of stride length) and increase the stroke frequency to achieve greater speeds (Costill et al., 1991). Horizontally swimming dolphins combine both patterns and increase stroke frequency linearly with speed while the distance per stroke remains relatively constant (Fig. 2). Mean distance per stroke was 2.4 m irrespective of speed. Stroke amplitude in dolphins also remained constant during horizontal swimming, with amplitude remaining at 20 % of body length for steady speeds ranging from 1.2 to 6.0 m s^{-1} (Table 2; Fish, 1993).

Buoyancy, gliding and energy expenditure during diving

Locomotor performance by horizontally swimming and vertically diving dolphins is influenced by very different physical factors. During horizontal swimming near the water surface, dolphins encounter high levels of drag associated with wave generation (Hertel, 1969). The effects of wave drag are negligible for diving dolphins once the animal is three body diameters below the water surface. Diving dolphins, however, face unique changes in buoyant forces with depth that become a major influence on performance and behavior.

An interesting finding in this study was the use of prolonged periods of gliding by dolphins for dives exceeding a depth of 50 m. Approximately 50 % of the descent phase was spent gliding rather than actively swimming on dives to a depth of 100 m. Deceleration rate decreased progressively during prolonged glides, finally reaching a point of zero deceleration at a depth of 90 m (Fig. 6B). These extended glides occurred only during the descent phase of deep dives (Fig. 4), suggesting that physical factors rather than distance *per se* dictated glide performance. Changes in buoyancy with depth due to lung compression from increased pressure probably contributed to these results. In general, dolphins dive after inspiration and exhale upon surfacing, indicating that they dive with inflated lungs (Ridgway et al., 1969; present study). Goforth (1986) reported that the diving lung volume of dolphins was approximately 75 % of maximum lung volume. The bronchi and trachea as well as the alveoli of the cetacean lung are collapsible, as determined in pressure chamber tests. Only the bony nares, with a volume of 50 ml, are rigid (Ridgway et al., 1969). Such a morphological structure permits a progressive collapse of the thorax with increased pressure at depth.

Compression of the air spaces in dolphins decreases volume without an accompanying reduction in mass. As a result, the dolphin becomes less buoyant with depth. Although it was not possible to measure directly the volume of air in an actively diving dolphin, the range of lung volumes and their effect on buoyancy have been determined for excised lungs from a 200 kg bottlenose dolphin (Ridgway et al., 1969). Ridgway and Howard (1979) calculated that alveolar collapse is complete once bottlenose dolphins experience pressures equivalent to 65–70 m in depth. The theoretical changes in buoyant force associated with this collapse are shown in Fig. 6. The maximum respiratory volume of the dolphin (11 l) was associated with neutral to slightly buoyant forces at full inflation and with a negative buoyancy of 10 kg when the lungs were deflated. In the present study, we found that changes in the deceleration rate of gliding dolphins were similar in pattern to the calculated changes in buoyant forces with lung compression (Fig. 6), suggesting a correlation between pressure and locomotor movements at depth.

Using this basic information, we can examine the relationship between physical factors and the swimming behavior of dolphins during diving. Major physical forces include buoyancy, acting in an upward or downward direction depending on diving depth, and drag opposing the forward

Table 4. *Calculated energetic costs for overcoming drag and buoyancy during a 100 m dive by an adult bottlenose dolphin*

	Active swim distance (m)		Speed (m s^{-1})		Locomotor cost (J)
	Descent	Ascent	Descent	Ascent	Total
Measured	53	92	1.73	1.90	26 064
Neutral buoyancy					
Total time-fixed	95	95	1.76	1.76	28 608
Speed-fixed	95	95	1.73	1.90	31 465

Locomotor costs were determined from the product of net forces (Table 3) and distance traveled.

Measured values for a dolphin wearing an instrument package are compared with those for two models assuming neutral buoyancy. The time-fixed model maintains the total dive time to that measured for the diving dolphin. Swimming speed is adjusted to accommodate the time requirement. The speed-fixed model maintains the swimming speeds for ascent and descent to those measured for the diving dolphin. However, the duration of the dive is adjusted to accommodate the neutral buoyancy and speed requirements.

movement of the dolphin. For the straight-line trained dives in the present study, total body drag acts upwards as the animal descends and downwards relative to the motion of the dolphin during ascent. The combined effects of these forces during various segments of a 100 m dive by a bottlenose dolphin are presented in Table 3. For the instrumented dolphin, passive gliding predominated when the calculated net force opposing the animal was less than 21 N. If the opposing force was higher, prolonged gliding was untenable and the dolphin switched to either stroking or short periods of burst-and-glide swimming. This may explain in part the high proportion of gliding during vertical diving in comparison with horizontal swimming by the same animal. With no buoyancy advantage during horizontal swims, the calculated drag for the speed range examined exceeded 21 N, and little gliding occurred. As mentioned above, descending glides during long descents reached zero deceleration at depth of approximately 90 m depth. At this depth, the downward force imparted by negative buoyancy fully counteracted the calculated drag and provided the dolphin with a theoretical ‘free ride’.

Although the progressive negative buoyancy with depth provides a locomotor advantage during descent, the reverse occurs during ascent. The same force that pulled the dolphin down must be overcome for the animal to return to the surface, seemingly negating any benefit. If energetic and hydrodynamic factors are considered together, we find that gliding provides an overall advantage for the diver. This is due to a significant reduction in active drag, which contributes to the energetic efficiency of burst-and-glide swimming (Blake, 1983). The locomotor behavior of diving dolphins is analogous to a type of burst-and-glide swimming, with exceptionally long glides facilitated by changes in buoyancy with depth.

The energetic advantage of gliding may be determined theoretically by calculating the total energy expended to overcome drag and buoyancy (locomotor cost) in diving dolphins. We estimated locomotor costs from the product of the net forces and mean distance covered during gliding and swimming (Tables 3, 4). On the basis of the straight-line dives examined in this study, the locomotor cost for an instrumented dolphin performing a 100 m dive was 26 064 J (0.74 J kg^{-1} m^{-1}). This compares with a minimum locomotor cost of 0.73 J kg^{-1} m^{-1} calculated from the difference between maintenance costs and total minimum cost of transport for bottlenose dolphins swimming near the water surface (Williams et al., 1992; Williams, 1999). In view of the similarity in locomotor costs between these swimmers and divers, it is apparent that deep-diving dolphins select energetically efficient modes of locomotion. Despite the effect of the instrumentation (Figs 2, 5), the diving dolphins in the present study were able to match the predicted minimum locomotor costs of swimming dolphins by taking advantage of changes in buoyancy. The theoretical costs are considerably higher if we assume that dolphins are neutrally buoyant throughout the dive. If a dolphin were neutrally buoyant and tried to maintain the same dive duration for a 100 m dive, as measured in this study, then locomotor costs would increase by 10 %. A neutrally buoyant dolphin maintaining the same swimming speeds (with a consequent shorter dive duration) for a 100 m dive experiences a 21 % increase in energetic requirements (Table 4).

The reduction in active drag during gliding was the primary factor leading to the energetic savings during diving rather than changes in buoyancy *per se*. Because of the marked influence of the instrument package on body drag (Fig. 5), these calculations admittedly represent a conservative estimate of the effects of buoyancy on gliding performance. It is likely that uninstrumented dolphins will exhibit even greater gliding performance with potentially greater energetic savings than indicated in these calculations. The reduction in power requirements and hence energetic costs associated with gliding initially appears modest. However, the savings may provide a significant advantage to free-ranging dolphins by allowing extended foraging time through the conservation of limited energy stores.

In conclusion, the present study illustrates how the interrelationships between swimming mechanics, buoyancy and underwater behavior support energetically efficient locomotion in diving dolphins. Similar conclusions regarding buoyancy and performance have been reached for other marine animals, including free-ranging elephant seals (*Mirounga augustirostris*) (Webb et al., 1998), diving ducks (Lovvorn et al., 1991) and a variety of fish species (Alexander, 1990). Variation in glide performance facilitated by changes in buoyancy appears to be an important mechanism that enables marine mammals to conserve limited oxygen stores during submergence. A corollary to this study suggests that speed alone is a relatively poor indicator of aquatic effort and may be inadequate for assessing energetic costs in diving marine mammals. Both gliding and active swimming often occur at similar speeds. However, the energetic consequences of each may be very different.

This series of papers on the diving physiology of dolphins was inspired by the work of Gerald L. Kooyman; they are dedicated to him in celebration of his remarkable research career and influence on all comparative physiologists. This study was supported by an Office of Naval Research grant and ASSEE fellowship (N00014-95-1-1023) to T.M.W. The authors thank the many people that assisted in this study including the trainers and dolphins at the SPAWAR facility in San Diego and the Dolphin Experience in the Bahamas. Computer assistance by S. Collier at Texas A&M University is gratefully acknowledged. In addition, the authors appreciate the critical evaluation of this manuscript by S. Noren, D. Noren and S. Kohin and lively discussions with F. Fish. All experimental procedures were evaluated and approved according to animal welfare regulations specified by NIH guidelines. UCSC and SPAWAR Systems Center (San Diego) conducted institutional animal use reviews.

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THE DIVING PHYSIOLOGY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

III. THERMOREGULATION AT DEPTH

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Summary

During diving, marine mammals initiate a series of cardiovascular changes that include bradycardia and decreased peripheral circulation. Because heat transfer from thermal windows located in peripheral sites of these mammals depends on blood flow, such adjustments may limit their thermoregulatory capabilities during submergence. Here, we demonstrate how the thermoregulatory responses of bottlenose dolphins (*Tursiops truncatus*) are coordinated with the diving response. Heart rate, skin temperature and heat transfer from the dorsal fin and flank were measured while dolphins rested on the water surface, stationed 5–50 m under water and floated at the surface immediately following a dive. The results showed that heat flow ranged from 42.9±7.3 to 126.2±23.1 W m^{-2} and varied with anatomical site and diving activity. Upon submergence, heat flow declined by 35 % from the dorsal fin and by 24 % from the flank. An immediate increase in heat flow to levels exceeding pre-dive values occurred at both sites upon resurfacing. Changes in heart rate during diving paralleled the thermoregulatory responses. Mean pre-dive heart rate (102.0±2.6 beats min^{-1}, *N*=26) decreased by 63.4 % during dives to 50 m and immediately returned to near resting levels upon resurfacing. These studies indicate that heat dissipation by dolphins is attenuated during diving. Rather than challenge the diving response, heat transfer is delayed until post-dive periods when the need for oxygen conservation is reduced.

Key words: dolphin, *Tursiops truncatus*, diving, heat flow, thermoregulation.

Introduction

Dolphins and whales are highly specialized marine mammals that spend their entire life at sea. One of the greatest physiological challenges to these marine endotherms is thermoregulation (Irving, 1969; Whittow, 1987). To counterbalance the high thermal conductivity of water, cetaceans have developed thick insulating blubber layers that encase the body. Thermal windows in poorly insulated peripheral areas permit the transfer of excess heat during periods of high activity or when the ambient water is warm (McGinnis et al., 1972). Integral to the function of these thermal windows is the vascular system, which plays an important role in the thermoregulatory responses of cetaceans (Fig. 1). For example, whales and dolphins maintain a counter-current arrangement of blood vessels in their flukes, dorsal fins and pectoral fins that provides fine control over the movement of warm blood between the body core and peripheral areas (Scholander and Schevill, 1955). Direct vascular links have also been reported for the dorsal fin and flukes of dolphins and for the temperature-sensitive reproductive organs (Rommel et al., 1994).

In addition to its thermoregulatory function, the vascular system of marine mammals plays a major role during the dive response. Marine mammals initiate a suite of physiological changes upon submergence to conserve oxygen and to support prolonged periods of breath-holding (Scholander, 1940; Elsner, 1969; Zapol et al., 1979; Kooyman, 1989). Collectively termed the dive response, these changes include a rapid, dramatic redistribution in blood flow that emphasizes the brain, lungs and heart. Apnea, bradycardia and a reduction in blood flow to peripheral sites (e.g. flippers and fins) are hallmarks of this response. These respiratory and cardiovascular adjustments, while facilitating oxygen conservation during submergence, may compromise the thermoregulatory function of thermal windows located in peripheral sites. Thus, an apparent conflict exists between oxygen conservation and heat dissipation during diving that results from the multiple roles played by the cardiovascular system of marine mammals.

To determine the effect of the dive response on

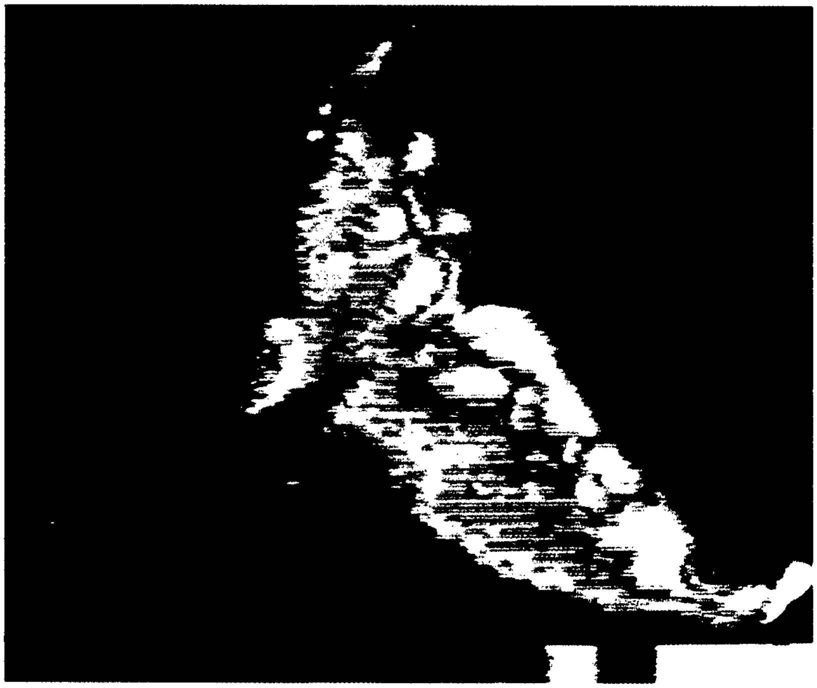

Fig. 1. Infrared thermograph of the fluke of a bottlenose dolphin. Warm areas (denoted by white and red) correspond to large blood vessels that traverse the width of the underside of the fluke. Note the comparatively cool peduncle area shown in blue. The color bar at the bottom denotes 0.1 °C differences in surface temperature per gradation.

thermoregulation in marine mammals, we monitored heat flow, skin temperature and heart rate during open ocean dives by trained bottlenose dolphins. These first recordings of heat transfer for an actively diving cetacean show that the thermoregulatory responses of dolphins depend on the phase of the dive. Heat flow from both peripheral and central sites was attenuated during submergence. The greatest period of heat transfer occurred immediately following a dive and corresponded to the release of the cardiovascular system from the dive response.

Materials and methods

Animals

Four adult Atlantic bottlenose dolphins (*Tursiops truncatus*, mean body mass 213 kg) were used in the heat flow studies. An additional immature dolphin was used for comparison during skin temperature measurements. The animals were maintained in large (15 m×15 m×4 m deep) saltwater enclosures connected to the open ocean in Freeport, Grand Bahama Island, Bahamas. Each animal was fed a daily diet of capelin, silversides and herring supplemented with multi-vitamins (Sea Tabs, vitamins C and B-12). Mean water temperature during the experimental period was 29.4 °C. Air temperature was 32.0 °C. Two adult, female Pacific bottlenose dolphins (*Tursiops tursiops gilli*, mean body mass 189 kg) were used in the diving heart rate tests. The animals were held in open-water, floating pens (7 m×7 m×3 m deep) in Kaneohe Bay, Oahu, Hawaii, and fed 2–3 times daily on mackerel, herring and smelt supplemented with vitamins. Average water temperature in the pens was 24.6 °C during the experimental period. Air temperature was approximately 28.0 °C.

Experimental design

Experiments were conducted on adult dolphins that had been acclimated to seasonally warm water temperatures ranging from 24 to 29 °C. Measurements were taken during three phases of the dive cycle: (1) at rest prior to diving, (2) during submergence, and (3) at rest on the water surface within 90 s of a dive. Resting measurements were made on quiescent animals as they floated near the water surface. Measurements on the diving dolphins were conducted in the open ocean approximately 1 nautical mile (1.85 km) offshore. On each experimental day, one or two dolphins followed a motorboat (17 or 21 foot Boston Whaler) from their enclosures to the dive site. Total swimming time was less than 15 min. During the heart rate studies, dolphins performed straight-line dives to a depth of 50 m while wearing a heart rate microprocessor placed on a harness. To avoid potential changes in thermal responses due to instrumentation (Wilson et al., 1986), heat flow and skin temperature measurements were conducted on separate dives. During the thermal studies, the dolphins accompanied a team of 3–4 SCUBA divers to depths ranging from 5 to 18 m. Trainers stationed the animal at depth and placed a heat flow/thermistor probe on the dorsal fin, fluke or flank. Experimental sessions lasted 20–50 min, depending on water depth. The dolphins periodically returned to the water surface to breathe between individual thermal measurements, while the SCUBA divers remained submerged for the entire session.

Heat flow and skin temperature

Heat flow across the skin of the dolphin to the surrounding water was measured using a 25 mm diameter disc-style heat flux transducer (Thermonetics Corp., San Diego, CA, USA) held against the stationary animal. The transducer was calibrated using a guarded heat plate procedure (ASTM C177) prior to and after experimentation. Briefly, the transducers were placed on a central heater in which the power input was continuously monitored. Once stabilized, the heater output was compared with the millivolt output signal of the transducer. The heat flux transducer is impervious to water, and its calibration is stable for several years. Transducer calibrations changed by less than 8.2 % over a 5 year period. Zero and range calibrations were conducted immediately before each experimental session; the zero calibration was rechecked during the dive by placing the probe in open water before measurements were taken. The accuracy of the instrument was ±0.1 mV (0.8 W m^{-2}).

A thermistor implanted in the transducer permitted simultaneous measurement of skin temperature during the heat flow measurements. The thermistor was calibrated before and after the experimental period using a digital thermometer (Physitemp, model Bat-12) placed in an insulated water bath ranging in temperature from 15 to 40 °C. Both the thermistor and the digital thermometer were also calibrated against a National Bureau of Standards mercury thermometer. The accuracy of the thermistor was ±0.1 °C. The accuracy of the thermistor was also tested against the digital thermometer placed on human skin and immersed in water. Thermistor readings on human skin were verified daily before each experimental session with dolphins.

The heat flux transducer/thermistor probe was mounted on a spring attached to a polyvinylchloride handle that allowed water to pass freely across the back of the transducer. The unit was held against the skin of the dolphin until the transducer stabilized and a steady-state signal was recorded for more than 20 s. Typical heat flow measurements required 1–2 min to complete and depended on the anatomical site. The response time of the thermistor was faster than that of the heat flux transducer and ranged from 10 to 50 s for stabilization depending on the temperature differential between the skin and water. Millivolt signals from the heat flux transducer and thermistor were recorded on two hand-held digital voltmeters (Micronta Multi-Mate). The voltmeters were placed in a weighted, clear acrylic waterproof box (Ikelite) when measurements were taken at depth. A 5 m line from the transducer probe handle was connected to the box and voltmeters by a submersible connector.

Anatomical sites representing peripheral thermal windows (dorsal fin, fluke, pectoral fin) and central areas (flank, peduncle) were measured. All measurements were taken with the probe completely submerged and represent skin temperatures and heat transfer from the surface of the animal to the water. For dolphins resting on the water surface either before or after a dive, the anatomical site of interest was submerged by approximately 12 cm during the measurements. Because of the equilibration time of the instruments and the breath-hold capability of the dolphins, it was not possible to measure heat flow and skin temperature for all sites during each dive session. Heat flow was recorded for the dorsal fin and flank during resting and diving. Skin temperatures were recorded for five different sites during resting and for the dorsal fin, fluke and flank during diving.

Heart rate

During heart rate sessions, the dolphins wore a nylon harness containing a heart rate/dive depth microprocessor (2.5 cm diameter × 15 cm long; Wildlife Computers, Inc.; Woodenville, WA, USA) and two cross-chest surface electrodes (Williams et al., 1993, 1999). The dolphins were trained to dive in a straight-line path between the boat and a submerged target positioned at a depth of 50 m. Heart rate from electrocardiographic signals was averaged over 10 s intervals throughout the dives. In addition, we monitored heart rate for 2 min periods immediately before and after the dives. Dive depth and duration were recorded simultaneously by the microprocessor at 1 s intervals. Data from the microprocessors were downloaded to a personal computer following each diving session and analyzed for changes in heart rate in relation to dive depth and duration using Dive-Analysis software (Wildlife Computers, Inc.; Woodenville, WA, USA). To ensure the accuracy of the heart rate microprocessor and electrode sensitivity, we periodically tested average heart rates from the microprocessor against values determined from electrocardiograph (ECG) waveforms (Birtcher Heart Rate Monitor, model 365) for dolphins resting on the water surface.

Statistical analyses

Data for skin temperature, heat flow and heart rate are presented as mean ±1 standard error of the mean (S.E.M.) unless indicated otherwise. Differences between means for heat flow during resting and diving were tested by two-way analysis of variance (ANOVA). Differences in heat flow and skin temperature between anatomical sites were determined from Tukey pairwise comparisons or Student's *t*-tests according to Zar (1974) using statistical software (Sigma Stat 2.0, Jandel Scientific, Inc.). Heart rate was calculated by dividing the total number of ECG waveforms or fractions thereof by the test interval according to Chabot et al. (1989). Significance is set at $P<0.05$ unless otherwise indicated.

Results

Heat flow

The level of heat flow from both central and peripheral sites depended on the phase of the dive cycle (Fig. 2). Heat flow from the surface of bottlenose dolphins ranged from 42.9±7.3 W m^{-2} for the flank during diving to 126.2±23.1 W m^{-2} for the dorsal fin immediately following a dive. In general, heat transfer was attenuated during submergence (two-way ANOVA factor dive, $F_{2,133}=14.9$, $P<0.001$), with transfer from the dorsal fin and flank decreasing significantly from pre-dive resting values (Tukey pairwise multiple-comparison test, pre-dive *versus* submerged, $P<0.05$). Upon resurfacing, heat flow from both sites immediately increased to levels above resting. Heat flow from the dorsal fin, a thermal window, was consistently higher than for the flank

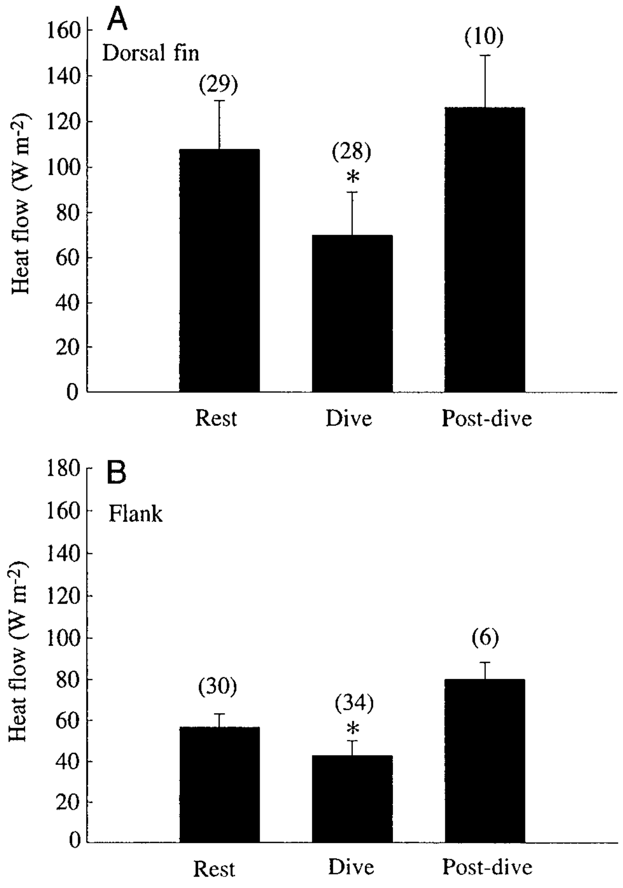

Fig. 2. Heat flow during resting, diving and post-dive periods for adult bottlenose dolphins. Values for the dorsal fin (A) and flank (B) are compared. Columns and vertical lines represent the mean values + S.E.M. Numbers in parentheses indicate the number of measurements in each data set for four dolphins. An asterisk denotes a significant decrease in heat flow between resting and diving values at $P<0.05$.

during all phases of the dive ($P<0.05$). In addition, the relative change in heat flow upon submergence was greater for the dorsal fin than for the flank (Fig. 2).

Skin temperature

Surface skin temperature of the dolphins remained within 1 °C of ambient water temperature (T_{water}) during resting and diving (Fig. 3). No significant difference (at $P<0.05$) was found between skin temperatures measured for five different anatomical sites of dolphins resting on the water surface. Measurement sites included both insulated central areas (flank, peduncle) and peripheral thermal windows (fluke, dorsal fin and pectoral fin). In contrast to the resting condition, mean skin temperatures of the peripheral sites (fluke and dorsal fin) were 0.4–0.6 °C lower than measured for the flank of diving dolphins. However, the values for these sites were not statistically different for either the resting or diving ($P=0.47$) dolphins.

Heart rate

Heart rate during the different phases of the dive changed in parallel with heat flow (Fig. 4). During the pre-dive period, the heart rate of bottlenose dolphins ranged from 72 to 120 beats min^{-1} (102.0±2.6 beats min^{-1}, $N=26$). The variability in resting heart rate was attributed to the apneic respiratory pattern of dolphins (Williams et al., 1993). In dolphins freely diving to a depth of 50 m, average heart rate decreased to 37.4±1.3 beats min^{-1} ($N=47$) within 50 s of submergence. An anticipatory tachycardia during ascent was followed by a mean post-dive heart rate of 93.0±3.1 beats min^{-1} ($N=15$). This pattern of prompt bradycardia followed by an anticipatory tachycardia during free diving has been observed for a variety of marine mammals, including free-ranging elephant seals (Andrews et al., 1997), Weddell seals (Hill et al., 1987), sea lions (Ponganis et al., 1997) and grey seals (Thompson and Fedak, 1993) as well as Pacific bottlenose dolphins trained to

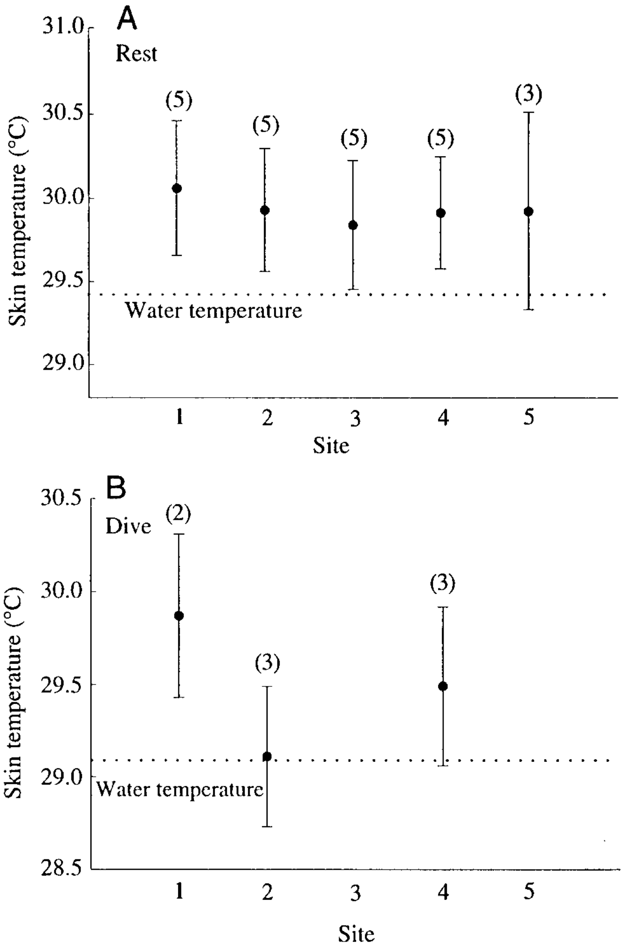

Fig. 3. Skin temperature for different anatomical sites of resting (A) and diving (B) bottlenose dolphins. Mean values ± 1 S.E.M. are presented. Numbers in parentheses represent the number of measurements in each data set for up to five dolphins. Anatomical sites are as follows: 1, dorsal fin; 2, mid flank; 3, mid peduncle; 4, underside of the fluke; and 5, underside of the pectoral fin. The horizontal dashed lines represent the water temperature at the measurement location (i.e. holding pen temperature for resting studies and ocean temperature at the dive site for the diving measurements).

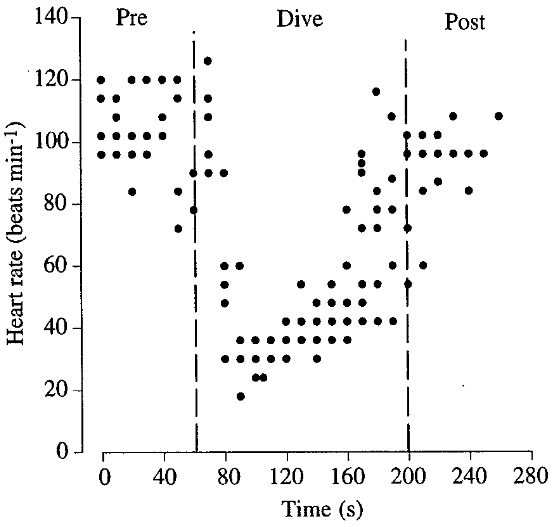

Fig. 4. Heart rate in relation to pre-dive, dive and post-dive intervals for two bottlenose dolphins. Data for six dives to a depth of 50 m are presented. Each point represents the average heart rate for 10 s intervals. Note the immediate bradycardia on submergence and the anticipatory tachycardia as the animal completes the dive.

dive in pools (Elsner et al., 1966) and the open ocean (Williams et al., 1999).

Discussion

The effects of diving on thermoregulatory responses in dolphins

Previous investigations of heat transfer in active cetaceans have focused primarily on the effects of water temperature or swimming exercise on heat loss (Hampton et al., 1971; McGinnis et al., 1972; Hampton and Whittow, 1976; Kasting et al., 1989; Ryg et al., 1993). In general, these studies have demonstrated that the dissipation of excess body heat in odontocetes (toothed whales) is greatest from peripheral areas, such as the dorsal fin, fluke and pectoral fins, and comparatively lower along the well-insulated flank. The difference in heat transfer between peripheral areas and insulated central sites depends on water temperature (McGinnis et al., 1972) and level of activity (Ryg et al., 1993). Interestingly, increased heat transfer occurs with relatively small changes in skin temperature (Fig. 3; see also Cuyler et al., 1992). Acclimation to ambient water temperatures also influences the level of heat transfer in cetaceans through changes in the thickness and quality of the insulating blubber layer (Worthy and Edwards, 1990; Williams et al., 1992). We find that the level of heat flow from the flank of warm-acclimated dolphins at T_{water}=24–29 °C (Fig. 2B) is similar to values for another odontocete, the killer whale (*Orcinus orca*), acclimated to T_{water} =12–18 °C (Kasting et al., 1989).

The results from this study demonstrate that diving activity introduces another important factor that influences the level of heat dissipation in odontocetes. Marked changes in heat flow occur upon submergence and resurfacing in diving dolphins (Fig. 2). These changes presumably result from the initiation and termination of the dive response, as manifest by alterations in heart rate (Fig. 4). In view of this, the thermal costs of odontocetes can easily be overestimated if based solely on measurements taken while the animal is on the water surface.

The inter-dive surface interval appears to be an important thermoregulatory period for diving marine mammals. By coordinating periods of elevated heat transfer with the release from bradycardia between dives, these animals can maintain the metabolic benefits associated with the dive response while meeting thermoregulatory demands. The bottlenose dolphins in the present study used the surface interval between short dives to transfer excess heat quickly to the environment. Weddell seals use the same inter-dive period to dissipate heat and to reduce core body temperature prior to sustained dives (Hill et al., 1987). Calculations by these investigators indicate that a pre-dive decrease in core temperature below resting levels may reduce the rate of oxygen consumption of central organs by 10–20 % in seals. As a result, the ability to transfer heat quickly while on the water surface may allow marine mammals to extend their total aerobic dive time.

Precise timing of heat transfer and the coincident control of organ temperatures during submergence are components of the thermoregulatory response of many diving marine endotherms. Weddell seals (Hill et al., 1987), bottlenose dolphins (Rommel et al., 1994) and king penguins (Handrich et al., 1997) show regional heterothermy and variable core temperatures associated with aquatic activity. As found for bottlenose dolphins in the present study, a temporal delay in thermoregulatory functions during the dive response allows many of these animals to accommodate two seemingly conflicting physiological requirements.

One consequence of the delay in heat transfer for diving bottlenose dolphins is a theoretical increase in core temperature during the course of the dive. Previous studies have shown that this odontocete exhibits rapid increases in core temperature during activity, especially under warm water conditions (McGinnis et al., 1972; Rommel et al., 1994; T.M.W., personal observation). Although it was not possible to monitor the core temperature of the dolphins in the present study, such an increase in core temperature during diving contrasts with other marine mammals. For example, it has been suggested that the low core temperatures of diving pinnipeds serve as a mechanism for reducing metabolic demands and conserving oxygen (Hill et al., 1987). Without data, it is difficult to know the magnitude of change in core temperature that may occur in diving dolphins. Larger size and shorter dive durations in comparison with those of phocid seals (Williams et al., 1999) and low activity levels facilitated by gliding during diving descents (Skrovan et al., 1999) may lead to only modest changes in core temperature. Obviously, further studies are needed to understand the effect of diving and delayed heat transfer on organ and core body temperatures in dolphins.

The thermoregulatory patterns of dolphins, like hypometabolism in diving marine mammals (Elsner and Wickham, 1988), may represent a specific example of a generalized mammalian response to resource limitations. Although temporal scales differ, analogous delays in heat transfer may be found in large terrestrial mammals such as desert-dwelling camels. Common to these animals is the limited availability of a critical resource. For diving dolphins, cardiovascular changes to conserve oxygen (Scholander, 1940) subsequently reduce heat transfer from thermal windows during submergence (Fig. 2). Similarly, dehydrated camels will reduce heat transfer during daylight hours to conserve water that would otherwise be lost in evaporative processes. Excess heat is stored until evening, when transfer can occur *via* non-evaporative pathways (Schmidt-Nielsen et al., 1957). With the availability of the limiting resource (oxygen in the case of dolphins, water for desert camels), heat transfer is elevated. Thus, we find that average heat flow is only 65.0 % of resting values for diving dolphins and 53.5 % of resting values for camels without access to water. When the limiting resource is available, heat flow is increased to 117 % and 168.3 % of resting levels for the dolphin and camel, respectively. This strategy of alternating periods of suppressed and elevated heat transfer allows both species to delay heat transfer until it can be accomplished with the greatest economy in specific resources.

In summary, this study demonstrates that heat transfer in bottlenose dolphins is attenuated by the dive response. While these results are somewhat intuitive because of the well-known cardiovascular changes associated with submergence, they illustrate how two potentially conflicting physiological responses are coordinated in diving marine mammals. An important benefit of this coordination between physiological processes is the potential for conservation of limited oxygen reserves.

This series of papers on the diving physiology of dolphins was inspired by the work of Gerald L. Kooyman: they are dedicated to him in celebration of his remarkable research career and influence on all comparative physiologists. This study was supported by grants from the Office of Naval Research (N00014-95-1-1023) and UCSC COR to T.M.W. The authors also thank the trainers at the Dolphin Experience (Freeport, Grand Bahama Island) and NOSC (Kaneohe, HI) for assisting with the diving dolphins. R. Davis, R. Skrovan, S. Noren and D. Noren provided invaluable comments on various drafts of the manuscript. All experimental procedures involving animals followed NIH Guidelines and were evaluated and approved by institutional Animals Use Committees.

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THE ROYAL
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The evolution of cost efficient swimming in marine mammals: limits to energetic optimization

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Mammals re-entered the oceans less than 60 million years ago. The transition from a terrestrial to an aquatic lifestyle required extreme morphological and behavioural modifications concomitant with fundamentally different locomotor mechanisms for moving on land and through water. Energetic transport costs typically reflect such different locomotor modes, but can not be discerned from the fossil record. In this study the energetic challenges associated with changing from terrestrial to aquatic locomotion in primitive marine mammals are examined by comparing the transport, maintenance and locomotor costs of extant mammals varying in degree of aquatic specialization. The results indicate that running and swimming specialists have converged on an energetic optimum for locomotion. An allometric expression, $\mathrm{COT_{TOT}} = 7.79\ \mathrm{mass}^{-0.29}$ ($r^2 = 0.83$, $n = 6$ species), describes the total cost of transport in $\mathrm{J\ kg^{-1}\ m^{-1}}$ for swimming marine mammals ranging in size from 21 kg to 15 000 kg. This relation is indistinguishable from that describing total transport costs in running mammals. In contrast, the transitional lifestyle of semi-aquatic mammals, similar to that of ancestral marine mammals, incurs costs that are 2.4–5.1 times higher than locomotor specialists. These patterns suggest that primitive marine mammals confronted an energetic hurdle before returning to costs reminiscent of their terrestrial ancestry, and may have reached an evolutionary limit for energetic optimization during swimming.

Keywords: swimming; energetics; transport cost; marine mammals; locomotor evolution

1. INTRODUCTION

The evolutionary pathway of marine mammals involved transitions from terrestrial specialists to intermediate forms capable of moving both in air and water, and from these intermediate forms to aquatic specialists (Repenning 1976; Berta *et al.* 1989; Thewissen *et al.* 1994). These transitions were associated with morphological, physiological and behavioural modifications to overcome the disparate physical demands of locomotion through two different media. Since water is 800 times denser and 60 times more viscous than air (Dejours 1987) the transition from terrestrial to aquatic locomotion undoubtedly challenged the mechanical and physiological systems of ancestral marine mammals.

Many of the morphological transitions that led to proficiency in the aquatic environment are revealed in the fossil record. Fossil cetaceans (*Ambulocetus natans*) and pinnipeds (the Enaliarctidae, *Potamotherium*) demonstrate transitional forms within these lineages (Repenning 1976; Berta *et al.* 1989; Thewissen 1994; Thewissen *et al.* 1994) and reflect a continuum for locomotor optimization in marine mammals. Common to these ancestral marine mammals was a locomotor apparatus that supported movements on land and in water. For example, the limbs of transitional pinnipeds and cetaceans were more robust than they are in extant species. Flexibility of the axial skeleton in transitional mammals also suggests the capability for undulatory propulsion when submerged. Thus, *Ambulocetus* probably resembled a swimming otter in water and a shuffling sea lion on land (Fordyce & Barnes 1994; Thewissen *et al.* 1994). Likewise, the skeletons of *Potamotherium* (Repenning 1976) and *Enaliarctos mealsi* (Berta *et al.* 1989) indicate both otter-like and seal-like locomotor patterns for archaic pinnipeds.

Despite revelations about locomotor mechanisms, the fossil record has provided little insight into the coincident physiological constraints and challenges that accompanied the transitions in morphology and lifestyle. Differences in the mechanics of running and swimming as well as in the thermal properties of air and water would demand different energetic inputs as mammals evolved into aquatic forms. Here, I examine the energetic consequences of such transitions by comparing maintenance and locomotor costs, and the total cost of transport of extant mammals varying in degree of aquatic specialization. Extant terrestrial, semi-aquatic and marine mammals were considered representative of principal evolutionary hallmarks within marine mammal lineages. A comparison of transport costs for these transitional and specialized groups of mammals provided an opportunity to assess the energetic consequences of evolving aquatic locomotion from terrestrial building blocks. The results from this study indicate that running and swimming specialists have converged on an energetic

Table 1. *Energetic costs and swimming speeds of mammalian swimmers*

(Oxygen consumption was determined for animals resting water prior to exercise and during steady-state swimming. Measurements on active animals were done as the subjects swam against a water current in a flume or unrestrained in open water. Oxygen consumption (mlO_2 kg^{-1} min^{-1}) was converted to metabolic energy (Joules, J) assuming a caloric equivalent of 4.8 kcal per litre of O_2 and a conversion factor of 4.187×10^3 J kcal^{-1}. Minimum COT_{TOT} was determined from the lowest oxygen consumption during swimming divided by speed. Criteria for data selection from the literature included: (i) use of respirometry methodologies for measuring metabolic rates of resting and active animals; (ii) steady-state metabolic levels during measurements; and (iii) non-diving conditions.)

species	mass (kg)	$\dot{V}O_{2rest}$	$\dot{V}O_{2swim}$	COT_{TOT} (J kg^{-1} m^{-1})	speed (m s^{-1})	method
		(mlO_2 kg^{-1} min^{-1})				
semi-aquatic						
muskrat[b]	0.6	14.7	48.0	21.4	0.75	flume
North American mink[c]	1	20.0	97.5	41.1	0.75	flume
sea otter[d] (surface)	20	13.5	29.6	12.6	0.8	flume
(submerged)	20	13.5	17.6	7.4	0.8[a]	flume
human[e] (elite front crawl	80	24.9	30.0	10.5	1.0	flume
(elite breast stroke)	80	24.9	53.1	16.8	1.0	flume
Marine						
California sea lion[f,g,h]	21	—	13.7	2.3	2.0	flume
	23	6.3	22.0	2.8	2.6	flume
	23	6.6	13.0	2.4	1.8	flume
harbour seal[f,i]	32	—	23.6	3.6	2.2	flume
	33	5.1	15.2	3.6	1.4[a]	flume
	63	4.6	9.6	2.3	1.4[a]	flume
grey seal[j]	104	7.7	15.0	3.9	1.3[a]	flume
bottlenose dolphin[g,k]	145	4.6	8.1	1.3	2.1	ocean swim
killer whale[l]	2738	—	—	0.84	3.1	field respiratory
	5153	—	—	0.75	3.1	rates
grey whale[m]	15 000	—	—	0.4	2.1	field respiratory rates

[a] Represents maximum flume speed. Minimum cost of transport speeds based on routine speed of free ranging animals is 1.0 ms^{-1} for submerged sea otters and *ca.* 2.0 ms^{-1} for phocid seals.
[b] Fish 1982.
[c] Williams 1983.
[d] Williams 1989.
[e] Holmer 1972.
[f] Williams *et al.* 1991.
[g] Present study.
[h] Feldkamp 1987.
[i] Davis *et al.* 1985.
[j] Fedak 1986.
[k] Williams *et al.* 1993.
[l] Kriete 1995.
[m] Sumich 1983.

optimum during locomotion that may represent an evolutionary limit for mammals.

2. ASSESSING ENERGETIC COSTS IN SWIMMING MAMMALS

(a) *Metabolism during rest and activity in water*

Metabolic rates have been determined for a variety of swimming mammals that differ markedly in propulsive style. The range of subjects include marine mammals specialized for aquatic locomotion and semi-aquatic mammals that routinely move both on land and in water (table 1). Maintenance costs (MC) of aquatic mammals are assessed from the rate of oxygen consumption ($\dot{V}O_2$) measured on quiescent animals floating quietly under metabolic hoods or breathing into gas-collection bags. To avoid elevations in metabolism associated with thermoregulation, water temperatures in the metabolic chambers are maintained at routine pool, pen, or ocean temperatures for individual animals (i.e. 12–25 °C for the subjects in table 1). Likewise, metabolic depression coincident with diving responses can be a complicating factor. When resting, semi-aquatic mammals such as minks (Williams 1983), muskrats (Fish 1982) and humans (Holmer 1972) remain on the water surface whereas marine mammals such as seals (Davis *et al.* 1985; Fedak 1986; Williams *et al.* 1991), sea lions (Feldkamp 1987; Williams *et al.* 1991) and dolphins (T. M. Williams, unpublished data) alternate between floating and briefly submerging. The pinnipeds and cetaceans used in the present study submerged for only brief intervals (less than one minute). Therefore, none were considered to be in a diving state. Under these conditions MC includes the energy expended for basal functions as well as endothermy in the alert animal.

Except for cetaceans, the metabolic rates of swimming mammals are often determined on animals trained to swim against a current in a water flume (table 1). Flume dimensions must take into account the frontal area and propulsive movements of each species. In addition, water flows must provide a physiological challenge for the swimmer (Williams 1987). Most of the energetic data for swimming semi-aquatic mammals and smaller marine mammals have been obtained by using open-flow respirometry in conjunction with these flumes. Because most flumes are too small or too slow for studying cetaceans, exercise tests for swimming dolphins, killer whales and grey whales have used several novel approaches. These include measuring physiological parameters while trained bottlenose dolphins follow a moving boat at sea (Williams *et al.* 1993), and calculating metabolic costs from respiratory patterns of free-ranging killer whales (Kriete 1995) and grey whales (Sumich 1983). A critical feature of these methods is the ability to monitor the subjects at preferred steady state velocities as determined from the routine movements of wild animals.

When comparing the energetics of aquatic mammals it is important to distinguish between swimming and diving activities. In the context of this study, swimming refers to transit swimming in which the course of movement is generally in the horizontal direction and the animal has constant access to air. This differs from diving in which the subject undergoes an extended period of apnea and may initiate a suite of physiological changes including bradycardia, peripheral vasoconstriction and metabolic suppression associated with the dive response (Kooyman 1989). The synergistic metabolic effects of diving superimposed on swimming exercise are beyond the scope of the present study. Therefore, transport costs are compared for transit swimmers only.

(b) *Cost of transport and locomotor costs*

Schmidt-Nielsen (1972) defined the energy cost of locomotion as the amount of fuel it takes to transport one unit of body weight over a unit distance. In the literature, 'total mass specific metabolic rate of the exercising animal divided by speed', as well as, '(total mass specific metabolic rate of the exercising animal minus resting mass specific metabolic rate) divided by speed', have been used interchangeably to define the 'cost of transport'. The former describes the energy required by the individual animal to satisfy both maintenance and locomotor demands during exercise while the latter describes the amount of energy required for moving the body and limbs. These are often termed the total cost of transport ($\mathrm{COT_{TOT}}$) and net cost of transport ($\mathrm{COT_{NET}}$), respectively (Schmidt-Nielsen 1972).

Here, I present total cost of transport ($\mathrm{COT_{TOT}}$), maintenance costs (MC), and locomotor costs (LC) for terrestrial, semi-aquatic and marine species, where

$$\mathrm{COT_{TOT}} = \mathrm{MC} + \mathrm{LC}.$$

$\mathrm{COT_{TOT}}$ is calculated by dividing the total metabolic rate of the active animal by locomotor speed. For aquatic mammals, $\mathrm{COT_{TOT}}$ represents the energy expended for transit swimming to distinguish it from diving. The difference between $\mathrm{COT_{TOT}}$ and MC has been termed the locomotor cost, LC (Williams 1989). This value represents the energy expended by animals for swimming performance and is analogous to $\mathrm{COT_{NET}}$ presented for running mammals (Schmidt-Nielsen 1972). To provide a common basis for comparing $\mathrm{COT_{TOT}}$ between animals of different size or form of locomotion (Taylor *et al.* 1970), minimum $\mathrm{COT_{TOT}}$ for each species is presented (Williams 1987). Energetic costs for mammals are then compared with those of flying birds (Tucker 1973), and salmonid (Brett 1964) and thunniform (Dewar & Graham 1994) fishes.

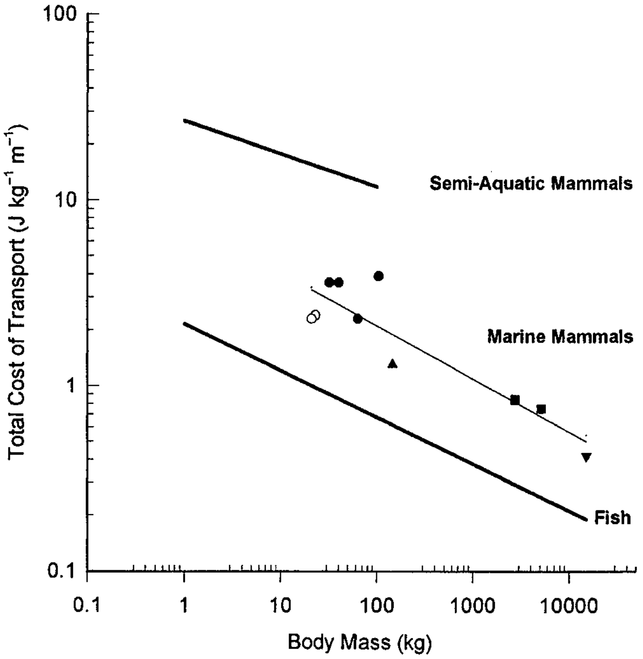

Figure 1. Total cost of transport ($\mathrm{COT_{TOT}}$) in relation to body mass for different classes of swimmers. Individual marine mammals are compared with regressions for semi-aquatic mammals and salmonid fish. Marine mammals include phocid seals (filled circles), California sea lions (empty circles), bottlenose dolphins (upward-pointing triangle), killer whales (squares), and grey whales (downward-pointing triangle) from table 1. The line through the data points is the least squares regression for marine mammals. The lower solid line represents the extrapolated regression for salmonid fish where $y=2.15x^{-0.25}$ (Brett 1964). The upper solid line shows the regression for swimming semi-aquatic mammals from Williams (1989) where $y=26.81x^{-0.18}$ and includes data for North American mink, muskrats, humans and surface-swimming sea otters.

3. DISCUSSION

(a) *Energetic costs incurred by swimmers*

The total cost of transport ($\mathrm{COT_{TOT}}$) for swimming mammals may be separated into two distinct groups distinguished by the degree of locomotor specialization (table 1, figure 1). As might be expected, a transitional lifestyle requiring movement between two media sacrifices energetic efficiency for versatility. Thus, semi-aquatic mammals such as minks and muskrats incur transport costs that are 2.4–5.1 times higher than observed for marine mammals (figure 1). Several factors, including hydrodynamic drag (Williams 1989) and propulsive efficiency (Fish 1993, 1996) undoubtedly contribute to the relatively high swimming costs of semi-aquatic mammals. In particular, elevated body drag associated with a surface-swimming position has a profound effect on transport costs. Theoretically, total drag is 4–5 times higher for a body moving on or near the water surface than for the same body submerged (Hertel 1966). This has been demonstrated for humans and harbour seals (Williams & Kooyman 1985), and sea otters (Williams 1989) by towing subjects on the water surface or submerged. Cardiovascular, respiratory and metabolic responses of swimming seals and sea lions also correspond to the percentage of time that the animal spends on the water surface or submerged while swimming (Williams *et al.* 1991). Similarly, the resulting transport costs for surface and submerged swimming sea otters reflect the differences in body position and drag (table 1).

The total cost of transport is comparatively low in mammals with increased specialization for one form of locomotion. Total transport costs in relation to body mass for swimming marine mammals ranging in size from 21 kg to 15 000 kg is described by

$$\mathrm{COT_{TOT}} = 7.79\,\mathrm{mass}^{-0.29} (r^2 = 0.83, n = 10),$$

where the total cost of transport is in J kg^{-1} m^{-1} and body mass is in kilograms. This relation expands the observations of Culik & Wilson (1994) and includes otariid and phocid seals, large and small odontocetes, and a mysticete whale (see figure 1). Swimming style in these animals ranges from dorso–ventral undulation in cetaceans (Fish & Hui 1991) to fore-flipper propulsion in otariids (Feldkamp 1987) and lateral undulation of paired hind flippers in phocid seals (Fish *et al.* 1988). In view of the diversity of propulsive styles, it appears that swimming mode has little effect on COT$_{\mathrm{TOT}}$ among marine mammals. Similar patterns have been reported for other locomotor groups. For example, transport costs do not vary greatly with the style of swimming in fish (Schmidt-Nielsen 1972, 1984; Bennett 1985), or with bipedal or quadrupedal performance in runners (Taylor & Rowntree 1973; Fedak & Seeherman 1979). Among semi-aquatic mammals, a single allometric expression also describes rowers, paddlers and humans performing the front crawl and breaststroke (Williams 1989).

Despite specialization for aquatic locomotion, the COT$_{\mathrm{TOT}}$ of marine mammals are considerably higher than predicted for fish of comparable size (figure 1). Values for pinnipeds including otariids and phocid seals are 2.3–4.0 times those predicted for fish. The COT$_{\mathrm{TOT}}$ of cetaceans ranges from 2.1–2.9 times the predicted values. Bottlenose dolphins show the lowest ratio between measured and predicted values within this range (Williams *et al.* 1993). Larger cetaceans such as the killer whale (Kriete 1995) and grey whale (Sumich 1983) demonstrate COT$_{\mathrm{TOT}}$ that are 2.2–2.9 times those predicted for salmonid fish.

MC, which reflect inherent differences in endothermy between mammals and fish, appear to account for the discrepancy in COT$_{\mathrm{TOT}}$ between these vertebrate groups (figure 2). Endogenous heat production results in a characteristic metabolic disparity between ectotherms and endotherms (Bartholomew 1977). Furthermore, MC for many species of aquatic mammals are exceptionally high owing to the high thermal conductivity of water (Irving 1973; Whittow 1987). Thus, the metabolic rates of many species of aquatic mammal resting in water are 1.7–2.4 times higher than those predicted from allometric regressions for terrestrial mammals resting in air (Kleiber 1975; Williams 1998).

By subtracting the energetic burden of endothermy, we can compare the locomotor costs of marine mammals and fish. In other words, we can compare the amount of energy these animals dedicate to moving their body and appendages through water. This is accomplished by subtracting the MC determined for animals resting in water from its corresponding COT$_{\mathrm{TOT}}$. The resulting LC for many species of pinniped and cetacean resemble those predicted from the allometric relation for salmonid fish (figure 2). Values for sea lions and dolphins are within 11% of predictions; even the sea otter, when swimming submerged, shows LC approaching the expected value for fishes. Adult harbour seals are somewhat higher at 58% over predicted while grey whales are lower by 32%.

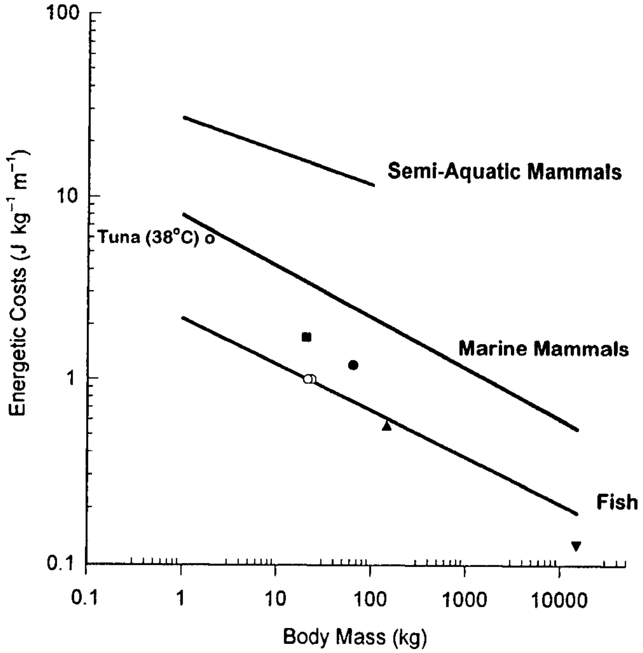

Figure 2. Locomotor costs of marine mammals compared with COT$_{\mathrm{TOT}}$ of different classes of swimmers. Solid lines are the allometric regressions for COT$_{\mathrm{TOT}}$ of semi-aquatic mammals, salmonid fish and marine mammals as in figure 1. Data points represent the mean locomotor costs (LC) for different species of marine mammal including sea otters (square), California sea lions (plain circle), harbour seals (filled circle), bottlenose dolphins (upward-pointing triangle) and grey whales (downward-pointing triangle). Data are from sources cited in figure 1. The calculated COT$_{\mathrm{TOT}}$ for swimming tuna (bold circle) at 38 °C (Dewar & Graham 1994; Dewar *et al.* 1994) is provided for comparison.

The energetic costs of endothermic fish also support these findings. Countercurrent heat exchangers allow many species of tuna to conserve metabolic heat and achieve periods of endothermy (Dewar & Graham 1994). Consequences of this thermal specialization (and associated physiological and biochemical modifications) are higher maintenance and transport costs in comparison with ectothermic species. Thus, the COT$_{\mathrm{TOT}}$ for yellowfin tuna (*Thunnus albacares*, mean fork length = 51 cm) swimming at 25 °C is 2.75 J kg^{-1} m^{-1}; a value that is 56% higher than predicted for salmonids swimming at the same temperature (Dewar & Graham 1994). By using a Q_{10} of 1.67 determined for yellowfin tuna (Dewar & Graham 1994), we can calculate the theoretical COT$_{\mathrm{TOT}}$ for tuna swimming at a mammalian temperature of 38 °C. The resulting value is within 7% of the predicted COT$_{\mathrm{TOT}}$ for a similarly sized marine mammal (see figure 2). Although it is unlikely that a tuna would experience such an increase in core temperature (Dewar *et al.* 1994), these calculations serve to illustrate the pathways for evolutionary convergence associated with endothermy and cost efficient locomotion in large aquatic animals. Both mammals and fish are capable of locomotor thermogenesis, but it appears that the ability to retain endogenous heat dictates the difference in transport costs between these groups.

(b) *Comparisons with other mammalian athletes*

The disparate physical demands for moving on land, through water or through air result in perceptible differences in effort. Among elite animal athletes, evolution and training promote specialized body morphologies and locomotor mechanisms for each form of locomotion. Energetic transport costs usually reflect these specializations and the underlying physical demands of swimming, running and flying (Schmidt-Nielsen 1972; figure 3*a*). An interesting finding in the present study is the nearly identical allometric regressions describing $\mathrm{COT_{TOT}}$ for swimming in marine mammals and for running in terrestrial mammals (figure 3*b*). Rather than mode of locomotion, phylogenetic history appears to be an important factor in setting the total energetic cost of active mammals. Total cost of transport for running, swimming and even flying mammals can be described by a single allometric relation

$$\mathrm{COT_{TOT}} = 10.02\,\mathrm{mass}^{-0.31} (r^2 = 0.92),$$

where $\mathrm{COT_{TOT}}$ is cost of transport in $\mathrm{J\,kg^{-1}\,m^{-1}}$ and body mass is in kilograms ($n = 55$ individual values representing four species of bat, and 29 terrestrial and six marine mammal species). This relation is indistinguishable from regressions describing transport costs for mammals specialized for running or swimming; bats, however, show $\mathrm{COT_{TOT}}$ for flying that are slightly lower than predicted by this regression (figure 3*b*). Neither the slopes nor *y*-intercepts of the allometric regressions for obligate terrestrial or marine mammals are significantly different from the combined regression (table 2). An important factor in these energetic relations is specialization for one mode of locomotion. The allometric regression for semi-aquatic mammals is significantly different from that describing $\mathrm{COT_{TOT}}$ for terrestrial mammals (*y*-intercept $t_5 = 4.874$, $p < 0.005$; slope $t_5 = 3.113$, $p < 0.05$). In contrast, comparisons between the regressions for marine and terrestrial mammals demonstrate no significant differences for these locomotor specialists (*y*-intercept $t_8 = 0.558$, $p > 0.25$; slope $t_8 = 0.172$, $p > 0.25$). Thus, we find that the cost of running in a 28 kg goat is identical to the cost of swimming in a 32 kg harbour seal. A 24 kg running dog incurs costs that are only 6% higher. A 107 kg horse maintains a cost of transport within 25% of the cost of swimming for a 104 kg grey seal. $\mathrm{COT_{TOT}}$ for a swimming bottlenose dolphin approaches that of a running eland. By comparison, similarly sized semi-aquatic mammals incur costs that are 3–4 times higher.

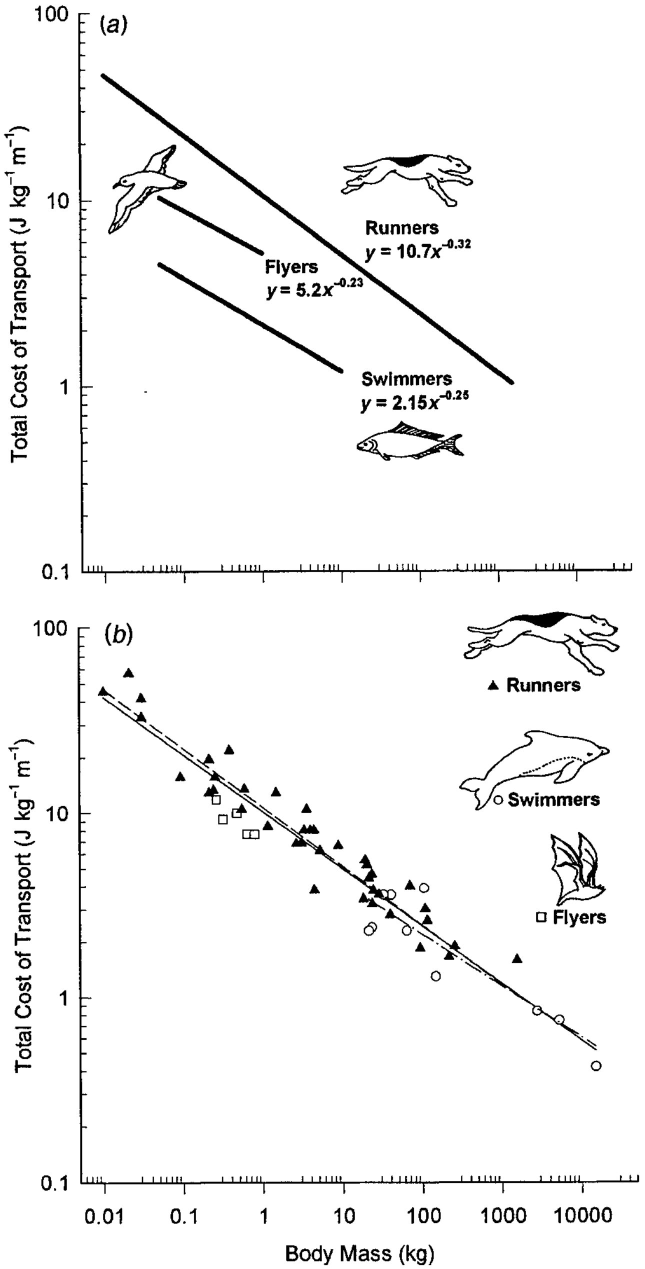

Figure 3. Total cost of transport in relation to body mass for different classes of vertebrates. The conventional comparison for swimming fish, running mammals and flying birds (*a*) is compared with swimming (open circles), flying (open squares) and running (filled triangles) mammals (*b*). (*a*) Regressions are from Tucker (1973) for flyers, Taylor *et al.* (1982) for runners, and Brett (1964) for swimmers, and is based on Schmidt-Nielsen (1972). (*b*) The solid line represents the $\mathrm{COT_{TOT}}$ regression for all mammals including flying bats ($n = 5$), swimming marine mammals ($n = 10$) and running terrestrial mammals ($n = 40$). Individual values in (*b*) are from Taylor *et al.* (1982) and Langman *et al.* (1995) for terrestrial mammals, Carpenter (1985, 1986) for bats and as in figure 1 for marine mammals. The dashed and stippled lines show allometric regressions for running and swimming mammals, respectively.

It is important to recognize that the relative energetic contribution of locomotor and maintenance processes to $\mathrm{COT_{TOT}}$ differs for mammals specializing in swimming, flying or running. In general, a greater proportion of the $\mathrm{COT_{TOT}}$ is comprised of maintenance costs for many marine mammals in comparison with terrestrial or aerial mammals (figure 4). For example, 22–77% of $\mathrm{COT_{TOT}}$ was comprised of maintenance costs in pinnipeds, sea otters, and bottlenose dolphins (table 1). This compares with only 12% in terrestrial mammals and 14% in bats. These results support the theoretical predictions of Peters (1983) who suggested that the higher total transport costs of swimming homeotherms in comparison with swimming poikilotherms was owing primarily to proportionately higher maintenance metabolic costs.

Table 2. T-*test statistics comparing the allometric regression describing transport costs for locomoting mammals*

(Costs for all locomoting mammals ($COT_{TOT} = 10.02\ mass^{-0.31}$, $n=55$, $r^2=0.92$) are compared to the regressions for swimming marine mammals ($COT_{TOT} = 7.79\ mass^{-0.29}$, $r^2=0.83$, $n=10$) and running terrestrial mammals ($COT_{TOT} = 10.7\ mass^{-0.32}$ from Taylor *et al.* 1982). Regressions for cost of transport versus body mass (log–log transformed) were determined using least squares methods (Zar 1974). Differences in the slopes and y-intercepts of allometric regressions for marine and terrestrial mammals, and for semi-aquatic mammals and locomotor specialists were evaluated. Regression parameters were computed from the sources and data in table 1 for marine and semi-aquatic mammals, and taken from the published literature for running mammals (Taylor *et al.* 1982) including elephants (Langman *et al.* 1995).)

	y-intercept	slope
terrestrial mammals		
t_{38}	1.6	0.5
$p>$	0.05	0.25
marine mammals		
t_8	0.42	0.13
$p>$	0.25	0.25

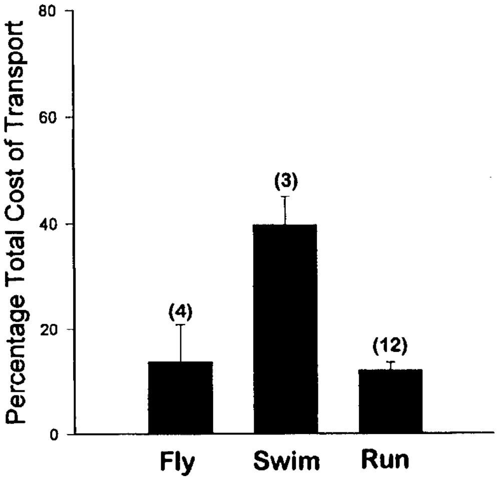

Figure 4. Percentage of COT_{TOT} attributed to maintenance costs in flying, swimming and running mammals. Height of the bars and vertical lines represent mean percentage of COT_{TOT} +1 s.e. for each group. Maintenance costs were determined from the metabolic rates of animals resting in air or water prior to exercise as described in the text. Data are from sources cited in figure 3. Numbers in parentheses represent number of species.

When LC and MC are taken into account, the results of this study remain consistent with previous studies concerning the relative energetic cost of swimming, flying and running (Schmidt-Nielsen 1972; Tucker 1975). That is, the cost of swimming is lower than that of other forms of locomotion (figure 3*a*). In mammals specialized only for swimming, LC rather than COT_{TOT} resemble the values predicted for fish (figure 2). The implication is that the energy dedicated to moving the body and limbs varies with locomotor mode and is most economical for swimmers. However, the total energetic cost (COT_{TOT}) incurred by the swimming marine mammal is much higher. It is this total cost that cannot be distinguished from values reported for mammalian runners and flyers (figure 3*b*). Viewed as the entire energetic demand required for moving from one place to another, COT_{TOT} takes on an ecological relevance. Free-ranging animals must contend with the total energetic expenditure associated with supporting basic biological functions as well as with moving the body and appendages through the environment. COT_{TOT} provides an indication of the sum of these expenses, and perhaps should be termed the excursion cost or ecological cost of transport (Garland 1983) to differentiate it from the standard usage of cost of transport.

(c) *Optimizing oxygen delivery during locomotion*

It is not intuitively obvious why the cost of swimming in fish should be lower than flight in birds and why both of these are energetically cheaper than running. Indeed, the high drag of the aquatic environment would have suggested the opposite. Runners must expend energy to overcome gravity, whereas swimmers overcome hydrodynamic drag, and flyers contend with both aerodynamic drag and gravity (Schmidt-Nielsen 1972). To date, it is unclear which of these, if any, posed the greatest evolutionary challenge to mammalian energetic pathways.

The similarity in total transport costs for terrestrial, aquatic and aerial mammalian specialists (figure 3*b*) suggests a physiological rather than mechanical limit for COT_{TOT}. Tucker (1975) indicated that the comparatively low mean muscular efficiency of running animals accounted for their higher costs of transport. Similarly, Taylor and colleagues (Taylor *et al.* 1980; Taylor 1987) have proposed that the observed differences in transport costs between swimmers, runners and flyers may result from differences in the cost of generating muscular force rather than in doing work against the environment *per se.* Variations in the energetic cost for size-specific recruitment of individual fibre types in skeletal muscles may also account for differences in transport costs (Rome 1992).

A closer examination of the two parameters used to calculate transport costs, locomotor velocity and the rate of oxygen consumption during exercise, provides additional insights regarding the costs for different modes of locomotion. The velocities associated with the minimum COT_{TOT} for different forms of locomotion do not follow the pattern observed for running, swimming and flying costs. Swimming fish and running mammals of comparable body mass tend to move at similar minimum COT_{TOT} speeds, whereas flying birds move considerably faster (Peters 1983). For example, fish ranging from 0.06 kg salmonids (Brett 1964) to 2.2 kg yellowfin tuna (Dewar & Graham 1994) swim at 0.30–1.1 $m\ s^{-1}$. Similarly sized mammals show minimum cost running speeds ranging from *ca.* 0.2 $m\ s^{-1}$ to 0.6 $m\ s^{-1}$ while similarly sized birds fly 15–30 times faster (Tucker 1973). Likewise, flying mammals move at 7–8 $m\ s^{-1}$ while terrestrial counterparts barely approach 0.6 $m\ s^{-1}$. The minimum COT_{TOT} speed is *ca.* 2.0 $m\ s^{-1}$ for many marine mammals regardless of the size of the swimmer (Videler & Nolet 1990; table 1). Yet, a sea otter-sized terrestrial mammal runs at 0.8 $m\ s^{-1}$ and a dolphin-sized terrestrial mammal shows a minimum COT_{TOT} speed of over 6.5 $m\ s^{-1}$ (Taylor *et al.* 1982). Based on the relative costs for swimming, flying and running (figure 3*a*), the order in which we would expect the fastest performances would be: fish, birds, and terrestrial mammals. Instead, flyers routinely outperform both runners and swimmers.

The ability of an animal to take in, deliver and translate oxygen into muscular work during exercise affords a qualitative explanation for the differences in $\mathrm{COT_{TOT}}$ for animals. Structural and functional variations along the respiratory system appear to correlate with limits in oxidative metabolism (Weibel *et al.* 1987; Taylor *et al.* 1987*a*). The diffusing capacity of the lungs, cardiac output, and capillary volume and total mitochondrial volume within the locomotor muscles are important factors in setting the aerobic capacity of terrestrial athletes (Taylor *et al.* 1987*b*). Comparable details are not available for the respiratory pathways of other vertebrate groups. However, comparisons of the efficiency of gas-exchange organs have been made for piscine, avian and mammalian systems. These studies indicate that the countercurrent gills of fish are the most efficient vertebrate respiratory system for extracting oxygen from the surrounding medium. This is followed by the cross-current system of birds and finally the open pool system of mammals (Piiper & Scheid 1982; Scheid 1982). Interestingly, the relative differences in $\mathrm{COT_{TOT}}$ for swimming fish, flying birds and running mammals (figure 3*a*) parallel the theoretical sequence in gas exchange efficiency among these vertebrate groups.

It is likely that the gas-exchange systems of these groups operate below their theoretical limits under normal physiological conditions (Scheid 1982). Yet, inherent differences in the efficiency of the oxygen pathway, whether at the level of the oxygen uptake, delivery or use by the skeletal muscles, could provide clues about the relation between physiological limits and the optimum energetic costs during locomotion. Mammals tend to preferentially select locomotor speeds that result in the lowest energetic cost (Hoyt & Taylor 1981). If the oxygen pathway operates at near maximum efficiency at these preferred speeds, then the similarity in $\mathrm{COT_{TOT}}$ for mammals regardless of whether they are swimming or running (figure 3*b*) is not as surprising.

Clearly, further research regarding the efficiency of the oxygen pathway for different mammalian groups is needed. In addition, it is difficult to predict if the same patterns will apply to other vertebrate groups. Evolutionary pressures as well as the malleability of the oxygen pathway may be very different for birds, lizards and fish, and warrant further investigation.

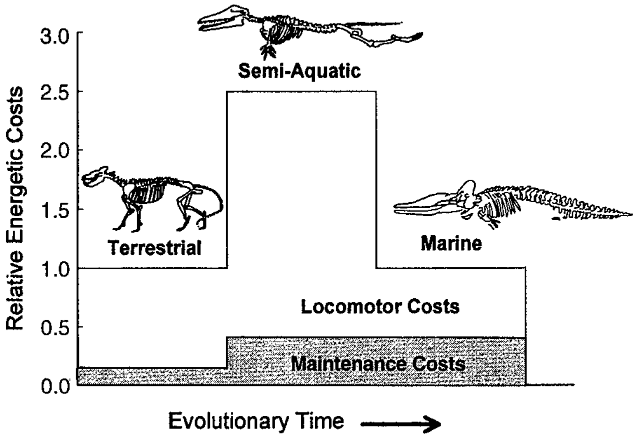

Figure 5. Theoretical changes in $\mathrm{COT_{TOT}}$, locomotor costs and maintenance costs with the evolution of fully marine living mammals. The evolutionary pathway assumes that ancestral marine mammals included an obligate terrestrial form that was followed by a semi-aquatic form (i.e. *Ambulocetus*) and finally an obligate marine form. The solid lines at the top denote relative $\mathrm{COT_{TOT}}$. The white and grey areas designate locomotor and maintenance costs, respectively. Note the similarity in $\mathrm{COT_{TOT}}$ for terrestrial and marine specialists despite the change in the relative contribution of locomotor and maintenance costs. (Skeletons redrawn from Berta 1994.)

(d) *The evolution of cost efficient swimming in mammals*

These results permit us to speculate about the energetic challenges faced by ancestral marine mammals. The physiological building blocks available to the first mammalian expatriates into the aquatic environment would have been those of a terrestrial specialist, i.e. a mammal designed primarily for moving on land. Assuming that the same physiological constraints act on extant mammals, the energetic trend during evolution would have been from the low transport costs of the terrestrial specialist to the high costs of amphibious species followed by a return to the initial low cost level in the aquatic specialist (see figure 5). With increased morphological specialization (Fish 1996), and consequently increased proficiency in the water, energetic costs for locomotion could be reduced. Thus, in evolving an aquatic lifestyle primitive marine mammals probably encountered and overcame an energetic hurdle in terms of transport costs only to return to energetic levels dictated by their terrestrial ancestry. Such an energetic hurdle initially seems counter to the argument that natural selection maximizes fitness along an evolutionary pathway. However, locomotor and physiological mechanisms are only part of the energetic equation for ancestral animals (Alexander 1996). The selective forces for entering the aquatic environment (i.e. favourable climatic conditions, ecological or habitat opportunities, the exploitation of previously untapped food resources; Fordyce 1989; Fordyce & Barnes 1994) undoubtedly provided an energetic benefit to the mammal. Presumably, these benefits surmounted the energetic difficulties associated with entering the water. Furthermore, limiting the duration of initial forays into the water may have reduced energetic disadvantages in the form of high maintenance and locomotor costs. This strategy is observed in extant semi-aquatic mammals such as the North American mink (*Mustela vison*; Williams 1986) and Australian water rat (*Hydromys chryogaster*; Fanning & Dawson 1980). By maintaining a labile core body temperature and limiting aquatic activity to short periods these mammals gain the energetic advantage of additional prey resources while minimizing energetic disadvantages. Consequently, minks and water rats establish an overall balance in costs and benefits by shuttling between energetic peaks and valleys. A similar mechanism in ancestral marine mammals would have relegated the proposed energetic hurdle to a transient phenomenon.

The resulting $\mathrm{COT_{TOT}}$ for extant marine mammals are higher than predicted for salmonid fish, but further evolutionary or energetic improvements are unlikely. Without the energetic burden of endothermy many marine mammals show locomotor costs approaching those of fish, a group that has the lowest cost of transport among vertebrates (Schmidt-Nielsen 1972). If, as these results imply, marine mammals have reached an energetic optimum in terms of locomotor costs, then $\mathrm{COT_{TOT}}$ may only be reduced by altering the comparatively high maintenance costs (figure 4). This may be accomplished by entering a hypometabolic state, an energy conserving strategy observed for some marine mammals during prolonged apneas associated with diving (Hochachka & Guppy 1987; Hurley 1996). Such a physiological mechanism may also explain the exceptionally low transport costs of submerged-swimming beavers (Allers & Culik 1997) and platypus (Fish *et al.* 1997).

Current evidence suggests that specialists among mammals have converged on an energetic optimum for locomotion. Unexpectedly, the phocid seals, otariids, odontocetes and mysticetes independently evolved into forms with swimming transport costs equivalent to those of running mammals. Regardless of the style of propulsion or locomotor mode (figure 3*b*), mammals appear to expend similar levels of energy to move a kilometre, albeit at different speeds and maintenance costs. This implies a preferred limit in aerobic efficiency along the pathway for oxygen in mammalian systems. Taylor and colleagues (1987*a*,*b*) have suggested that structural and functional limitations along this pathway dictate aerobic performance capacities in terrestrial athletes. The present study indicates that similar limitations may apply to aquatic mammals. To maximize performance within these limitations the energetically efficient swimmer will specialize for one locomotor event, and thus improve chances for successfully hunting prey, escaping predators or winning in Olympic competitions.

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BIOLOGY OF MARINE MAMMALS

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5

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Marine Mammal Energetics

Why study energetics? An understanding of energy flow through a single organism or a community made up of multiple organisms provides insight into the relative importance of the many biological and physical processes impinging on an animal. More important, it provides information about the interrelationship between an animal and the environment in which it lives. Energy flow models are analogous to cost–benefit models used in economics. Costs take the form of energy expended to acquire and process prey and to maintain body functions. The energetic benefits are manifest as the food energy used for growth and reproduction.

Because of their high rate of food consumption, marine mammal populations are often major components of energy flow models describing marine communities; a few individuals can have seemingly disparate impacts on their habitat. Examples include sea otter (*Enhydra lutris*) predation on benthic invertebrates (Riedman and Estes 1990), sperm whale (*Physeter macrocephalus*) foraging in the Gulf of Mexico (Davis and Fargion 1996), and the growing conflict between marine mammals and fishermen as they draw from the same fish resource. Models of energy flow enable us to understand the energetic impact of these mammals on marine communities. By measuring the various avenues of energy transfer we can determine how animals organize their daily or seasonal activities and how they prioritize their behaviors.

Patterns of energy acquisition and expenditure also provide insight into the unique strategies developed by marine mammals to survive and reproduce in an energetically challenging environment. To be an effective predator in the aquatic environment, marine mammals have undergone significant modifications of the "typical" mammalian physiology. Extreme examples are the ability of some marine mammals to fast for months at a time, subsisting entirely on energy stored in their extensive blubber. This mammalian group also demonstrates a remarkable ability to conserve thermal energy that might otherwise be lost in maintaining body temperature in the cold polar seas. Furthermore, precise budgeting of energy expenditure is crucial to enabling marine mammals to dive for more than 1 hr to depths in excess of 1500 m.

In this chapter we examine the major pathways of energy flow for marine mammals. The chapter is divided into two sections. In the first section, the basic physiological concepts of energy flow in mammalian systems are presented. We begin with a generalized energy budget, and then describe in detail four major areas of energy expenditure. These areas address the energetic costs associated with (1) maintaining basic biological functions, (2) thermoregulation, (3) activity and work, and (4) growth and reproduction. The ecological implications of energy exchange between the marine mammal and its environment are addressed in the second section. These are discussed in the context of field metabolic rates for free-ranging marine mammals.

Physiology of Mammalian Energetics

Energy Budgets

The basic pattern of energy flow can be described by the balanced growth equation where Ingestion = Egestion + Excretion + Respiration + Somatic growth + Reproductive growth. This relationship applies the first law of thermodynamics, which states that energy and mass are conserved. Consequently, what goes into an animal (ingestion) must come out in the form of growth, waste, or metabolic work. In such models the "currency" for income or expenditure is given in units of total energy (joules), or as a rate of energy production or utilization measured in watts (joules/sec). However, this relationship can be modified and the units adjusted (e.g., 1 calorie = 4.184 joules) accordingly to include all forms of material or energy transfer between an organism and the environment. Thus, we can examine the balance between calories ingested by an animal in different prey items versus the calories of heat generated by the mammal. By adding a rate factor, we can compare metabolic power input in watts to mechanical power output based on drag and swimming speed for an assessment of locomotor efficiency.

The growth equation shows us that marine mammals must achieve a dynamic balance between the costs of existence and their ability to acquire energy. Ultimately, both sides of the equation must balance. Yet, temporal delays in energy acquisition and expenditure are common, particularly among large marine mammals. In the short term an animal may not be able to obtain sufficient food energy when foraging or it may face periodic challenges that require expenditure of more energy than it can obtain. If a marine mammal cannot compensate for decreases in energy acquisition, it must either reduce its overall rate of energy expenditure or use stored energy reserves. Conversely, for growth and reproduction to occur, the animal must obtain considerably more energy than is required for the individual to survive.

How the balance in energy acquisition and expenditure is achieved differs for individual species and environments. For some species (sea otters, sea lions, and fur seals) very high rates of energy expenditure are met by high rates of energy acquisition. These animals may preferentially live in environments near-shore or upwelling regions where food is abundant (Costa 1993a, 1993b). Manatees (*Trichechus* spp.) represent the opposite extreme. These sluggish marine mammals demonstrate comparatively low existence costs and are able to survive on a low-quality diet. They have adapted to a diet of grasses that are in high abundance but of low quality energetically. Fortunately, they live in the climatically benign tropics where existence costs may be kept to a minimum.

These simple relationships suggest that marine mammals living in an energy-rich, benign (thermally neutral) environment have little trouble meeting their energy demands and should have significant amounts of energy available for growth and reproduction. If food is plentiful, then energy can be expended at a rapid rate. In contrast, if food is scarce or difficult to obtain, then the rate of energy expenditure must be reduced to match the lower rate of food energy input. The seasonal migrations of large cetaceans demonstrate this interrelationship between energetic demand, energy availability, and local productivity. Twice a year, gray whales (*Eschrichtius robustus*) migrate more than 4800 km (3000 miles) between the energetically demanding, but highly productive polar environment, to the warm tropics, where productivity is significantly lower. Although existence costs may be elevated in the polar regions, the ability to take advantage of the immense productivity associated with the sea ice during the polar summer appears to more than compensate. When confronted with the high energetic costs of reproduction and winter conditions, the whales opt for the more benign tropics. Prey availability may be low, but so too are the existence costs, especially for a large animal that is able to live for long periods off of stored energy reserves in the blubber.

A representative energy flow diagram for marine mammals is presented in Figure 5-1 and demonstrates the distribution of energy into the various physiological processes of the animal. Ingested energy may be liberated in feces (egestion) and urine (excretion), or used as metabolizable energy (ME). The ME may be stored for somatic and reproductive growth or expended through respiratory processes. Key processes include the energetic costs associated with basal metabolism, digestion (heat increment of feeding), thermoregulation, and activity (locomotion, grooming, feeding, etc.).

Energy Acquisition

Ingested Versus Digested Energy

A large component of the growth equation is related to the processing of the ingested food energy. As this relationship suggests, not all of the ingested material consumed is digestible and energy may be lost as egestion and excretion. The amount of the ingested food energy that can be assimilated across the gut is a function of the composition of the diet. Invertebrate prey (i.e., shrimp, krill, clams, mussels) are

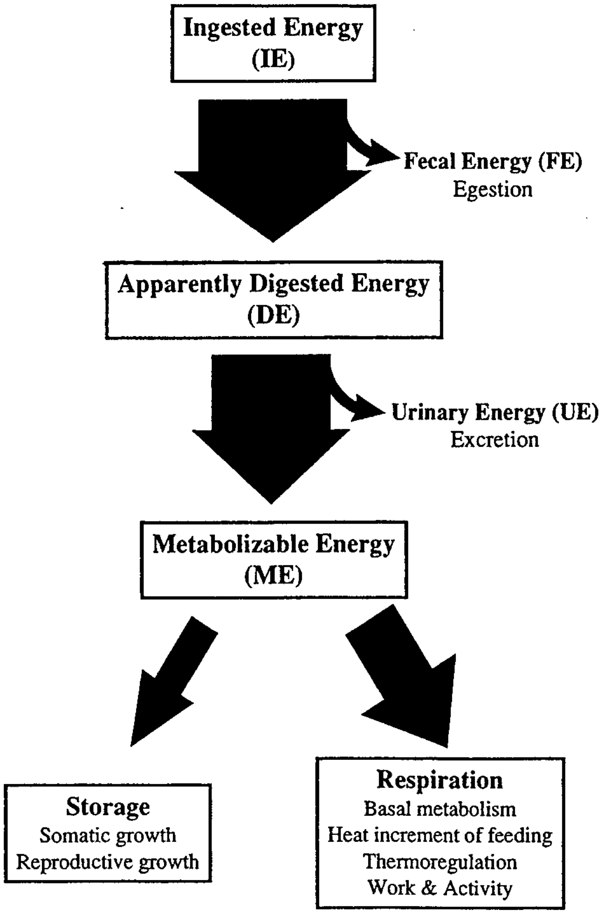


Figure 5-1. A generalized energy flow model for mammals.

important components of the diet of a wide variety of marine mammals from the smallest sea otters to the largest whales. These prey items often contain large amounts of indigestible components such as chitin in their exoskeletons. Foods that are high in fat are the most digestible (Kleiber 1975). Animal material is significantly more digestible than plant material because much of the energy in plants is in the form of cellulose, which vertebrates cannot digest without help from symbiotic microorganisms.

The ability of animals to digest a given prey item is termed the apparent digestibility (AD) and defined by the ratio of energy acquired during digestion and the energy consumed. It is typically presented as the percentage: Apparent digestibility = (Ingested energy – Fecal energy) / Ingested energy. The apparent digestibility of different diets for sea otters (Costa 1982) and pinnipeds has been examined. The ADs for herring (*Clupea harengus*) is 92.6% in gray seals (*Halichoerus grypus*) (Ronald et al. 1984), 93.8% in harp seals (*Phoca groenlandica*) (Keiver et al. 1984), and 97.1% in ringed seals (*Phoca hispida*). This increases slightly to 97.9% for ringed seals fed a diet of capelin (*Mallotus villosus*) (Parsons 1977). For northern fur seals (*Callorhinus ursinus*), AD ranges from 88% for diets consisting of capelin or squid (*Loligo opalescens*), to 90% for pollock (*Theragra chalcogramma*) and 90% to 93% for herring (Miller 1978, Fadely et al. 1990). Harbor seals (*Phoca vitulina*) show an AD of 92.1% and 96.7% for a diet of pollock or herring, respectively (Ashwell-Erickson and Elsner 1981). Polar bears (*Ursus maritimus*) have an AD of 91.6% when they consume ringed seals (Best 1976). Such relatively high AD is to be expected for animals eating prey that is low in fiber or chitin and is easily processed in the gut (Kleiber 1975). Invertebrate prey with a high chitin content, such as shrimp (*Pandalus borealis*), has a lower AD. Values for a shrimp diet average 72.2% for the harp seal (Keiver et al. 1984).

The high fiber and cellulose content of plant material results in a similarly low AD for the grazing manatee (Burn 1986); AD is reportedly 84.6% in the dugong (*Dugong dugon*) feeding on grasses (Murray et al. 1977). Sirenians use hindgut fermentation to fully digest plant material (Murray et al. 1977, Burn 1986, Reynolds and Rommel 1996). Interestingly, the AD of these animals are higher than the 45% to 59% measured for terrestrial mammals, such as the horse (*Equus caballus*), that use hindgut fermentation (Fonnesbeck et al. 1967, Fonnesbeck 1968). The AD of sirenians is similar to that measured for the green sea turtle (Bjorndal 1979). The high AD in sirenians also appears to be related to the low lignin content of aquatic vegetation and to the large body mass of the animal (Burn 1986, Reynolds and Rommel 1996). Large body size provides a comparatively large gastrointestinal tract and a low metabolic rate, which together allow a slow rate of passage of digesta and more efficient breakdown of fibrous plant material.

The ingested food energy (IE) is equivalent to the net chemical energy liberated as heat if food is completely oxidized. Food energy remaining after digestion and elimination of fecal energy (FE) is known as the apparently digested energy (DE) where IE = FE + DE or DE = IE × AD. Fecal energy includes the energy lost through the elimination of nonfood materials (i.e., intestinal secretions, microbes, and cellular debris); it is equivalent to the egestion term of the growth equation. It is important to note that the AD is given as a ratio, whereas the IE, FE, and apparently DE are given in quantitative units such as joules (J).

The chemical energy lost as the end product of metabolic processes is known as urinary energy (UE) and is equivalent to the excretion term in the growth equation. In mammals the most significant component of UE results from the urea formation, the end product of protein catabolism. In general, no UE results from the catabolism of fat or carbohydrate.

Metabolizable energy (ME) is the net energy remaining after fecal and urinary energy loss and represents the energy available to the animal for growth or supporting metabolic processes. In the growth equation ME is described by the energy available for work (locomotion), respiration (thermoregulation, maintenance metabolism, heat increment of feeding), as well as somatic and reproductive growth. Mathematically ME is described by: ME = IE – FE – UE.

The ME has been measured as a percentage of total energy ingested for California sea lions (*Zalophus californianus*) on a diet of herring (88.2%), anchovy (*Engraulis mordax*) (91.6%), mackerel (*Scomber japonicus*) (91.4%), and squid (78.3%) (Costa 1988a). This compares with the ME of 87.1% for harp seals (Keiver et al. 1984), 82.7% for gray seals (Ronald et al. 1984), and 89.8% for ringed seals (Parsons 1977) fed herring. Harbor and spotted seals (*Phoca largha*) fed either pollock or herring diets had a ME of 80.3% (Ashwell-Erickson and Elsner 1981).

Energy Expenditure

The Cost of Maintenance Functions

Maintenance costs are defined as the energy required to maintain constant body mass and composition (homeostasis). After fecal and urinary losses, the remaining energy must be sufficient to meet the energy costs of homeostasis. The cost of homeostasis includes basal metabolism, the heat increment of feeding, heat used for thermoregulation outside the zone of thermoneutrality, and heat liberated as voluntary activity (Fig. 5-1). As mentioned above, these components of energy flow can vary as a function of the proximate composition of the prey consumed and the animal's nutritional history.

BASAL METABOLISM. It has generally been assumed that the basal metabolic rates of aquatic mammals are elevated when compared to terrestrial mammals of similar size. This had been explained as an adaptation for maintaining thermal balance under conditions of high thermal conductivity when in water (Hart and Irving 1959, Kanwisher and Sundnes 1966, Irving 1973, South et al. 1976, Kanwisher and Ridgway 1983). The current view of marine mammal basal metabolic rates is more complex. Lavigne et al. (1986) identified one problem; many past studies assessing metabolic rate in aquatic mammals did not conform to standardized criteria established by Kleiber (1975) for comparing the basal metabolism of animals. These require that the subjects be adults, resting, thermoneutral, and postabsorptive.

Another confounding problem has been the assumption that all marine mammals use identical metabolic responses. Specialization for marine living has occurred in at least five mammalian lineages, the sirenians, cetaceans, pinnipeds, sea otters, and polar bears. On the basis of this diversity, we might expect different metabolic adaptations among the groups (Fig. 5-2). For example, manatees demonstrate basal metabolic rates that are lower than values predicted by the Kleiber relationship based on similarly sized terrestrial mammals (Scholander and Irving 1941, Gallivan and Best 1980, Irvine 1983). The basal metabolism of phocid seals appear to be equivalent to Kleiber predictions (Lavigne et al. 1986).

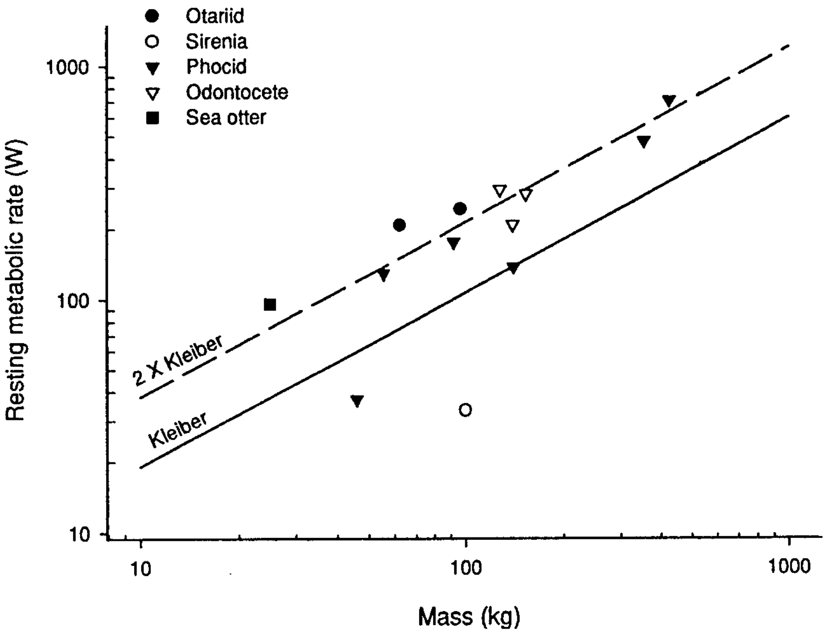


Figure 5-2. Resting metabolic rate (RMR) of marine mammals in relation to body mass. Measurements were made for the animals resting in water. The solid line denotes the predicted metabolic rate from Kleiber (1975); the dashed line represents two times the predicted levels. (The sources of data used in this figure are provided in the text.)

Conversely, data for sea otters, otariids, and odontocetes suggest that the basal metabolic rates of these mammals are greater than predicted for terrestrial mammals (Pierce 1970, Ridgway and Patton 1971, Morrison et al. 1974, Costa and Kooyman 1982, Costa et al. 1989b, Liao 1990, Hurley 1996).

Extreme differences in the body composition of marine mammals introduces another complicating factor when attempting to compare basal metabolic rates. Many species of marine mammal undergo large variations in body fat seasonally or in association with life history patterns (Rice and Wolman 1971, Costa et al. 1986). Some species, such as sirenians and walrus (*Odobenus rosmarus*), have dense bone. Because metabolic rates are conventionally expressed in terms of total body mass, a disproportionate amount of fat or particularly dense bone will lower the apparent metabolic rate. This is attributable to the low metabolic rates of bone and adipose tissue in comparison to lean tissue (Kleiber 1975). Thus, animals of equivalent body mass but different percentages of fat or bone display different metabolic rates. This relationship was confirmed in studies of northern elephant seal (*Mirounga angustirostris*) pups. The fat content of these pups increased from 4% to 48% between birth and weaning. When comparing various sized elephant seal pups, lean mass rather than total body mass was the better predictor of metabolic rate (Rea and Costa 1991).

The difficulty in establishing the basal metabolic rate of marine mammals is attributable in part to the definition of resting. Marine mammals appear at rest while bobbing on the water surface as well as while lying quietly submerged. The metabolic demands of each state may be very different due to physiological changes associated with the diving response (Elsner, Chapter 3, this volume). Recent studies on submerged, resting California sea lions suggest that the metabolic rate of these animals approaches basal values predicted for terrestrial mammals during prolonged periods of apnea (Hurley 1996). In view of this, we may need to redefine the criteria for assessing basal metabolism in marine mammals to conform with their unique lifestyles and physiology.

Costs Associated with the Heat Increment of Feeding

When food is consumed the animal's metabolic rate increases over fasting levels. This increase in metabolism results from the biochemical work associated with the digestion and chemical processing of food. Historically, the process has been referred to as specific dynamic action (SDA), although the recent convention is heat increment of feeding (HIF) (Kleiber 1975). The HIF may be considered the "tax" that is required to process food energy for conversion to ME. The magnitude of the energy allocated to HIF varies between 5% and 17% of the ME and is related to the composition of the diet. In addition, the duration of HIF after a meal will depend on the amount of food consumed and its composition (Table 5-1).

If we continuously monitor the metabolic rate of an animal after a meal, we find that metabolic rate slowly increases, reaches a peak, and then returns to the resting nonfed level. This metabolic bulge is often of sufficient magnitude that it must be taken into account in the analyses of energy metabolism. Expressed in terms of the energy content of the food consumed, HIF is about 6% for carbohydrates, 13% for fats, and 30% for proteins (Bartholomew 1977a).

Under experimental conditions, HIF is usually determined on animals placed in a thermally neutral environment. As a result, the excess heat resulting from HIF is dissipated from the body by thermoregulatory pathways and is considered "wasted" energy (Kleiber 1975). For free-ranging marine mammals or when thermoregulatory demands are high, HIF is an excellent mechanism for defraying high metabolic costs associated with keeping warm. The actively foraging marine mammal must contend with the constant thermal challenge of living in relatively cold water and heating ingested prey items. This can lead to an interesting balancing act between the energetic costs associated with HIF, activity, and thermoregulation. Rather than acting independently, the various components of the energy flow diagram (Fig. 5-1) may act synergistically to reduce the overall cost to the animal. For example, sea otters use heat generated from the digestion of food (HIF) to offset thermoregulatory costs when water temperature is low (Costa and Kooyman 1984).

The Cost of Temperature Regulation

Marine mammals maintain body temperatures within the typical mammalian range of 36° to 40°C. However, this is ac-

Table 5-1. The Heat Increment of Feeding (HIF) in Marine Mammals

Species/Diet	Increase HIF (%)	Duration of Above RMR	Diet Protein HIF (hr)	Content (%)
Harp seal[a]	17	1.67	7	
Harbor seal[b]	9.0			High
Herring	5.1	1.46	15	Low
Harbor seal[c]	4.7	1.28	10–12	
Elephant seal[d]		1.65	10.4	
Capelin	12.1			15.2
Herring	11.2			17.4
Sea otter[e]		1.54	4.2–5.3	
Clam	13.2			10.5
Squid	10.0			11.1

[a]Gallivan and Ronald 1981; [b]Markussen et al. 1994; [c]Ashwell-Erickson and Elsner 1981; [d]Barbour 1993; [e]Costa and Kooyman 1984.

RMR = resting metabolic rate.

complished under conditions of high heat transfer attributable the high thermal conductivity of water in comparison to air. Because heat flow may be 25 times greater in water than in air, marine mammals have evolved a wide variety of morphological and physiological adaptations to control heat loss to the environment. These include (1) an insulating layer comprised of blubber or fur; (2) thermal windows in poorly insulated peripheral sites; (3) complex vascular arrangements, which serve as variable heat exchangers, and (4) in some species, elevated basal metabolic rates (Scholander and Schevill 1955, Hart and Irving 1959, Kanwisher and Sundnes 1966, Irving 1969, Tarasoff and Fisher 1970, Hampton et al. 1971, McGinnis et al. 1972, Irving 1973, Hampton and Whittow 1976, Gallivan and Ronald 1979, Pabst, Rommel, and McLellan, Chapter 2, this volume).

Phocids, otariids, sea otters, and polar bears have the dual problem of thermoregulating in air when hauled out and in water during a wide variety of physiological states from rest to high-speed swimming. Conversely, cetaceans and sirenians are truly aquatic and avoid the conflicting thermoregulatory demands associated with an amphibious lifestyle. For many species of cetacean the primary thermoregulatory problem during rest is heat conservation. Even in waters at tropical temperatures small cetaceans such as Atlantic bottlenose dolphins (*Tursiops truncatus*) and the long-snouted spinner dolphin (*Stenella longirostris*) must guard against excess heat loss during rest (Hampton et al. 1971, McGinnis et al. 1972, Hampton and Whittow 1976). The findings of these investigators lend support to the hypothesis of Parry (1949) who inferred from his studies of the harbor porpoise (*Phocoena phocoena*) that small cetaceans are obliged to remain active, or to elevate their metabolic rate, to maintain thermal balance.

The aquatic environment represents a thermal energetic challenge for marine mammals. Consequently, these animals often depend on the energy produced by activity and feeding as well as marked control over peripheral insulation to maintain thermal balance (Hampton and Whittow 1976). For pinnipeds and cetaceans, a characteristic thermoregulatory feature is the extreme lability of their insulation (Kanwisher and Sundnes 1966, Hampton and Whittow 1976). Dorsal fins, flippers, and flukes act as thermal heat exchangers to afford considerable control in the regulation of body temperature.

THE THERMONEUTRAL ZONE. Surprisingly few studies have examined the thermoneutral zone (TNZ) of marine mammals in water (Fig. 5-3). The thermoneutral zone defines the range of environmental temperatures where metabolic heat production is minimal for the animal (Bartholomew 1977b). Its range is delineated by the lower and upper critical temperatures, T_{lc} and T_{uc}, respectively. Below the T_{lc}, physiological variations in thermal conductance are not sufficient to offset heat loss. Therefore, metabolism increases in accordance with decreases in environmental temperature (Schmidt-Nielsen 1979). Environmental temperatures that exceed the T_{uc} also result in an increase in metabolic rate, this time as a consequence of the additional work necessary to dump excess heat (Bartholomew 1977b).

Studies of the TNZ of marine mammals in water have concentrated on the phocid seals. In general, these pinnipeds demonstrate a broad TNZ when compared to the relatively narrow range of air temperatures representing the TNZ of terrestrial mammals. Irving and Hart (1957) and Gallivan and Ronald (1979) have shown that adult (150 kg) harp seals have a TNZ of at least 28°C. The T_{lc} is below 0°C, whereas the T_{uc} has yet to be defined. In harbor seals, the TNZ is

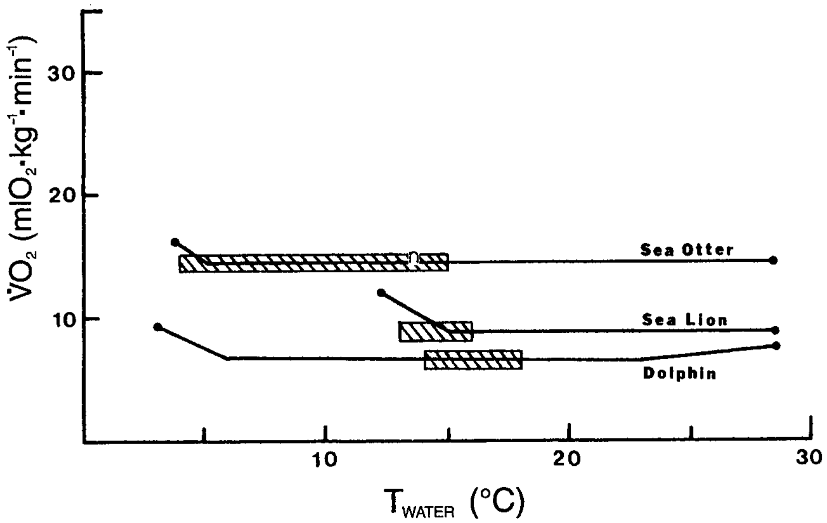


Figure 5-3. Oxygen consumption ($\dot{V}O_2$) in relation to water temperature for three species of marine mammals. Results for sea otters, sea lions, and bottlenose dolphins are compared. The horizontal portion of the line represents the thermoneutral zone (TNZ) for each species. The hatched box denotes the routine water temperature encountered by the animals in the wild. Note that the dolphins were acclimated to conditions in Hawaii, and the sea lions and sea otters to conditions off the California coast. (The sources of data used in this figure are provided in the text.)

dependent on both body size and season. The larger the animal, the lower the surface-to-volume ratio, and hence, smaller the surface area for heat loss. Large size may be associated with changes in the thickness of the blubber layer, which will also contribute to seasonal differences in the TNZ (Irving and Hart 1957, Hart and Irving 1959, Miller and Irving 1975, Miller et al. 1976). Thus, we find that harbor seals show a considerably higher T_{lc} (approximately 20°C) during the summer than when examined during winter (average $T_{lc} = 13$°C) (Hart and Irving 1959). The simplest explanation for this seasonal change is the 30% increase in insulation during the winter (Irving 1973).

In contrast to phocids, relatively little information exists on the variability of the thermoneutral zone of otariids. Sea lions are temperate water otariids and generally have a thinner blubber layer than arctic phocids of similar size (Bryden and Molyneux 1978). These animals appear to be ill-equipped for dealing with high environmental heat loads, often resorting to behavioral mechanisms for maintaining thermal homeostasis (Whittow et al. 1972). The T_{uc} for sea lions resting in air is between 22°C and 30°C, with smaller animals able to tolerate higher air temperatures than larger ones (Matsuura and Whittow 1973, South et al. 1976, Liao 1990). Once again we find a lower overall insulation and enhanced heat transfer as body size and blubber thickness decrease. With decreases in ambient temperature, sea lions will reduce blood flow to peripheral sites, which leads to an increase in total body insulation (Matsuura and Whittow 1975). This appears to be the primary thermoregulatory mechanism for sea lions until air temperatures decline below 10°C (Matsuura and Whittow 1973, South et al. 1976). Liao (1990) examined the metabolic responses of California sea lions to changes in water temperature (Fig. 5-3). The thermoneutral zone was approximately 20°C for this marine mammal resting in water, although the upper critical temperature was never identified. The T_{lc} of California sea lions was 14.8° to 16.4°C, at least 2°C above the range of water temperatures typically encountered by these animals in the wild (Fig. 5-3). This implies an increased reliance on physiological mechanisms of thermoregulation for these otariids.

Most studies of temperature regulation in small odontocetes have primarily concentrated on resting heat production, body temperature, and heat flow across the body surface (Irving et al. 1941, Kanwisher and Sundnes 1966, Irving 1969, Pierce 1970, Hampton et al. 1971, Ridgway and Patton 1971, Whittow 1987). Observations of elevated heat production and high tissue insulation in captive bottlenose dolphins and spinner dolphins indicate that they must conserve body heat, when at rest even in tropical waters averaging 24°C (Hampton et al. 1971, McGinnis et al. 1972, Hampton and Whittow 1976). Like California sea lions, these animals appear to live close to their critical temperatures and depend on the energy produced from activity and feeding as well as precise control of peripheral insulation to maintain thermal balance (Hampton and Whittow 1976).

Captive bottlenose dolphins acclimated to water temperatures averaging 28°C have a thermoneutral zone of at least 15°C. The upper critical temperature is near 28°C (Fig. 5-3). The T_{lc} depends on the thickness and quality of the blubber layer and the size of the cetacean. Larger animals or individuals with a thicker blubber layer have a lower T_{lc}. Therefore, the T_{lc} was 11°C for a dolphin with an average blubber thickness at more than 20 mm and 15°C for animals with thinner blubber layers (Costa et al. 1989a, Williams et al. 1993). Note that the range for the thermoneutral zone and upper and lower critical temperatures shift for dolphins acclimated to cooler water temperatures, similar to resetting the thermostat of a car for summer and winter conditions (T. M. Williams, pers. obs.).

Similar patterns are observed for wild dolphins. Seasonal changes in the body condition of dolphins in Sarasota Bay, Florida, include considerable variation in blubber thickness and total body fat. These changes undoubtedly reflect the dolphins' response to changes in water temperature. Blubber thickness averaged 18 mm for Sarasota Bay animals in winter acclimated to water temperatures of 16°C (G. A. J. Worthy, D. P. Costa, and R. S. Wells, unpubl.). The similarity in blubber depth for captive Hawaiian dolphins at 28°C and the wild Florida animals at 16°C seems contradictory. However, the quality of insulation as well as its depth need to be considered when assessing the thermal characteristics of the blubber layer (Williams et al. 1992). Worthy and Edwards (1990) found considerable differences in the blubber thickness and blubber fat content of harbor porpoises and spotted dolphins. Harbor porpoises living in cold coastal waters (average water temperature, 12°C) maintained blubber of lower thermal conductivity, $0.10 \pm 0.01\ \mathrm{W \cdot m^{-1} \cdot C^{-1}}$. In comparison, the thermal conductivity of blubber from spotted dolphins (*Stenella attenuata*) living in the eastern tropical Pacific Ocean (average surface water temperature, 27°C) was $0.20 \pm 0.02\ \mathrm{W \cdot m^{-1} \cdot C^{-1}}$. These variations were attributed to differences in the lipid content of the blubber layer. In addition, blubber thickness varied in harbor porpoises averaging 15 ± 3 mm, whereas spotted dolphin blubber averaged 7.7 ± 1.1 mm (Worthy and Edwards 1990). Consequently, insulating quality and quantity of dolphin blubber can be very different depending on species and routine environmental temperatures.

Unlike those of other marine mammals, the body temperatures of manatees, 35.6° to 36.4°C, are near the lower end of the normal mammalian range. With a T_{lc} of only 20° to 23°C (Gallivan et al. 1983, Irvine 1983), these mammals appear to have a low thermal tolerance to changes in water temperature. This physiological response limits the habitats that manatees can occupy to relatively warm regions. They rely on warm water refuges in the winter and may be susceptible to cold-related mortalities after periods of severe cold weather (Irvine 1983). With the notable exception of Steller's sea cow (*Hydrodamalis gigas*), sirenians as a group tend to have similar physiological limitations and are restricted to tropical habitats (Domning 1978, Marsh et al. 1978).

TEMPERATURE REGULATION DURING ACTIVITY IN WATER. Heat generated as a by-product of activity can alter the thermal energetic demands of the marine mammal. Just as a human running around a track on a cold day feels warmer than a sedentary friend seated in the bleachers, some marine mammals may use exercise-induced thermogenesis to help maintain a stable core body temperature when in cold water. The response depends on the balance between the level of heat production provided by activity and the elevation in convective heat loss associated with movements (Williams 1986).

Several studies on exercising California sea lions have shown conflicting results. Feldkamp (1985) demonstrated comparatively higher metabolic rates over a range of speeds for a juvenile sea lion swimming in water at 18°C than for animals swimming in water at 24°C. The metabolic response of these animals was similar to those observed for humans (*Homo sapiens*) (Nadel et al. 1974) and muskrats (*Ondatra zibethicus*) (Fish 1983) swimming at water temperatures below their TNZ. Conversely, Davis and Williams (1992) found that swimming speeds as low as 1 m/sec generated enough heat to defray the cost of thermoregulation in juvenile sea lions exercising in water temperatures ranging from 5° to 20°C. The conclusions of this study are similar to those presented for sea otters by Costa and Kooyman (1984) in which the level of activity was directly correlated with water temperature. Although these results are inconclusive, they do reveal a potentially important thermoregulatory strategy for marine mammals that warrants further investigation.

The Cost of Work and Activity

Whether a mammal lives on land or ice, or in the water, performing work is energetically expensive. As a result, the cost of locomotion or activities such as grooming, predatory maneuvers, and defending territories can be major components of an animal's total daily energy budget. This is not because these activities necessarily make up a large proportion of time, but because they exact a high metabolic cost. For example, the metabolic rate of an adult sea otter resting in water at 20°C is 12 to 13 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ (Costa and Kooyman 1982, Williams 1989). Grooming activity including fur pleating and rubbing, and somersaulting raises the otter's metabolic rate to more than 20 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$. Swimming on the water surface at a leisurely 0.8 m/sec increases the metabolic rate to nearly three times resting levels with even higher metabolic rates occurring when the sea otter swims faster (Williams 1989).

The aerobic scope (AS) provides a physiological measure of an animal's upper metabolic and performance limits. Defined by the ratio: Aerobic scope = Maximum oxygen consumption ($\dot{V}O_{2max}$)/Resting oxygen consumption ($\dot{V}O_{2rest}$), the aerobic scope is usually determined by measuring the minimum and maximum rates of energy metabolism under a standard set of conditions (Bartholomew 1977b). For locomotor studies the ratio is often set by the resting metabolic rate and peak metabolic rate during sustained muscular work.

In general, aerobic scope for activity in marine mammals is less than that measured for terrestrial mammals (Fig. 5-4). Running mammals typically show aerobic scopes between 10 and 25. Therefore, the maximum oxygen consumption ($\dot{V}O_{2max}$) during running is 10 to 25 times the level of oxygen consumption for the same animal standing quietly on a treadmill. The better the athlete or training, the greater the aerobic scope (Taylor et al. 1980). Many trained domestic and wild canids and thoroughbred racehorses show aerobic scopes on the high end of this range. In contrast, swimming marine mammals rarely demonstrate aerobic scopes above 6. This includes a variety of pinnipeds exercising in swimming flumes (Davis et al. 1985, Williams et al. 1991), harbor seals and a spotted seal treading water in a tank (Elsner 1987), and bottlenose dolphins swimming against a force platform (Williams et al. 1993). These comparatively low aerobic scopes do not imply that marine mammals are in poorer athletic shape than their terrestrial counterparts. Many factors including the level of maximum oxygen consumption measured during aquatic exercise and the definition of resting metabolic rate for marine mammals may account for the observed differences in AS. The $\dot{V}O_{2max}$ for the bottlenose dolphins exercising against a force platform was 30% to 40% lower than predicted values based on running mammals. Similarly, $\dot{V}O_{2max}$ for the phocid seals treading water was 40% lower than that predicted for a same sized terrestrial mammal. Low $\dot{V}O_{2max}$ levels during aquatic activity are not limited to marine mammal species. Humans achieve a $\dot{V}O_{2max}$ during swimming that is 11% to 19% lower than measured for the same athlete running on a treadmill. The $\dot{V}O_{2max}$ of the American mink (*Mustela vison*), a semiaquatic mammal, is 3% to 14% lower than for the same animals running on a treadmill (Williams 1983). Respiratory constraints and the utilization of smaller skeletal muscle mass during swimming exercise are possible causes for the relatively low $\dot{V}O_{2max}$ of mammals during swimming exercise.

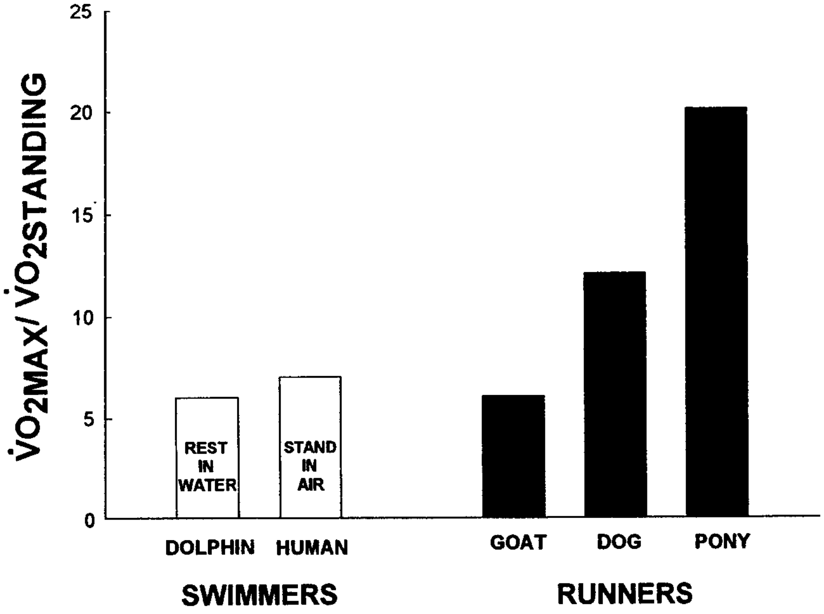


Figure 5-4. The dynamic aerobic scope ($\dot{V}O_{2max}/\dot{V}O_{2std}$) for swimming and running mammals. $\dot{V}O_{2std}$ was measured for dolphins resting in water and for the other species standing in air. Note the similarity in scope for swimming dolphins, swimming humans, and sedentary terrestrial mammals (goats).

Difficulties in defining the standard or resting metabolic rate of marine mammals also lead to complications in calculating aerobic scope in this group of animals. As mentioned in the preceding section, "resting" in marine mammals may range from bobbing on the water surface to lying submerged in apnea and bradycardia. The metabolic rates associated with each of these states may differ two- to threefold resulting in significantly different estimates for aerobic scope. If we use the predicted mammalian standard metabolic rate from Kleiber (1975), the resulting AS for dolphins pushing against a force platform ranges from 7 to 11. These levels are typical of relatively sedentary terrestrial species as described by Taylor et al. (1987), which conflicts with the athletic image of leaping dolphins and breaching whales. The general diving response of marine mammals may also preadapt this group to lower apparent aerobic scopes. In seals adaptations for hypoxia tolerance during submergence, an enhanced capacity to buffer pH shifts associated with lactate accumulation, and high oxygen storage capacities in the skeletal muscles, blood, and lungs may support greater metabolic efforts than indicated by traditional measurements of aerobic scope (Elsner 1986). To cope with a limited aerobic scope, marine mammals may also preferentially rely on anaerobic metabolism during high work loads. In this respect, exercising dolphins and seals appear similar to running lions (Williams et al. 1993). Obviously, further research is needed concerning the appropriate measurement and definition of upper and lower limits of metabolism in marine mammals.

SWIMMING CAPABILITIES. It is important to remember that marine mammals were originally equipped with the same physiological and morphological building blocks for locomotion as terrestrial mammals. The fossil record for cetaceans (Gingerich et al. 1994, Thewissen et al. 1994), pinnipeds (Berta et al. 1989), sea otters (Riedman and Estes 1990), and sirenians (Barnes et al. 1985), demonstrates their terrestrial ancestry. However, marine mammals show a variety of physiological, morphological, and behavioral adaptations that enable them to move quickly and efficiently through water. Consequently, aquatic performance by pinnipeds, cetaceans, and even sea otters far outranks our best Olympic athletes in terms of speed and energetic cost. Most humans rarely swim more than 1.0 m/sec, although elite human athletes attain swim speeds approximately two times faster. During the 1996 Summer Olympics, Amy Van Dyken won the gold medal for the women's 50-m free-style sprint with a swimming speed of 2.0 m/sec. The gold medal winner in this event for men, Aleksandr Popov, swam even faster at 2.3 m/sec. In comparison, the routine cruising speeds of many marine mammals approach the 2.0 m/sec swimming sprint speed of humans (Table 5-2). Northern fur seals, Galapagos sea lions (*Zalophus californianus wollebaeki*), Galapagos fur seals (*Arctocephalus galapagoensis*), and New Zealand sea lions (*Phocarctos hookeri*) demonstrate mean surface swimming velocities ranging from 0.6 to 1.9 m/sec (Ponganis et al. 1990). A similar range is observed for sustained submerged swimming by sea otters (Williams 1989) and northern elephant seals (Le Boeuf et al. 1992). Sustained swimming speeds are somewhat faster for cetaceans. For example, the range of sustained speeds for bottlenose dolphins is 1.4 to 3.1 m/sec depending on the duration of effort, depth, and behavior (Lang and Norris 1966, Würsig and Würsig 1979, Shane 1990, Williams et al. 1993). Free-ranging killer whales (*Orcinus orca*) average 2.4 m/sec (Kriete 1995),

Table 5-2. General Characteristics of Marine Mammal Swimmers

Characteristics	Sea Otter	Otariid	Phocid	Cetacean
Hydrodynamics	Surface	Submerged	Submerged	Submerged/porpoising
Mechanics	Paddle/row, dorsoventral undulate	Pectoral	Lateral thunniform with lunate tail	Dorsoventral thunniform
Stroke frequency[a] (strokes/min)	20–80 (surface) 56 (submerged)	15–50	60–78	60–90
Speed (m/sec)	< 1.4	2.0–6.0	2.0–6.0	2.0–10.0
Energetics				
$\frac{\text{Measured COT}}{\text{Predicted COT}}$	12 (surface) 6 (submerged)	4	4	2–3

[a] Values are for adult southern sea otters (Williams 1989), immature sea lions (Feldkamp 1987), harbor seals (Davis et al. 1985), and adult bottlenose dolphins (Williams et al. 1993).

COT = cost of transport.

whereas migrating bowhead whales (*Balaena mysticetus*) average 1.4 m/sec depending on their migratory route (Würsig et al. 1985). Sprinting speeds for both pinnipeds and cetaceans may be three to five times higher than these cruising speeds. Some otariid species reach 4.0 m/sec (Ponganis et al. 1990), whereas trained bottlenose dolphins have been clocked at more than 7.5 m/sec (Lang and Norris 1966), a speed that human swimmers have little hope of ever approaching. Even more remarkable than the high performance capabilities of marine mammals is the comparatively low energetic cost associated with swimming, as addressed in the following sections.

HYDRODYNAMICS. To understand the energetics of swimming in marine mammals, we have to appreciate the underlying hydrodynamics, that is the physics associated with propelling a body through water. A brief description is provided here with more detail found in Pabst et al. (Chapter 2, this volume). Fish (1993) also provides an excellent overview of the effects of body design and propulsive mode on swimming energetics in semiaquatic and marine mammals.

When a body moves through a fluid, a force acts backward on it, resisting its forward motion. Anyone who has waded knee deep in water or mud has experienced the increased effort needed to overcome this force. The resistive force, termed drag, is described by the equation:

$$\text{Drag} = 1/2r\rho V^2 ACd,$$

where ρ = the density of the fluid, V = velocity of the fluid relative to the body, A = body area, and Cd = drag coefficient. For mammalian swimmers, the most critical term in this equation is velocity squared, which causes drag to increase exponentially for every incremental increase in swimming velocity. Thus, the amount of work that the marine mammal must expend to move through the water increases exponentially with its forward velocity. This has a profound effect on both the energetics of swimming and the preferred swimming speeds of marine mammals.

Total body drag of harbor seals, sea otters, and humans has been measured by towing the subjects through water at different velocities. Drag forces for all subjects increased curvilinearly with towing speed (Fig. 5-5). The value of body streamlining in reducing drag is readily apparent if we compare the total body drag of humans to those of marine mammals. Drag on the submerged human form is 3 to 10 times that of the submerged seal (Williams and Kooyman 1985) or sea otter (Williams 1989) measured at comparable speeds. Limb internalization, an overall decrease in surface projections, and the approximation of an elongate, tapered hull contribute to the streamlined character of marine mammals. The result is lower body drag and a decreased energetic demand on the swimmer.

There are several components comprising total body drag of a swimmer. These include viscous drag and pressure drag, which are affected by the swimmer's surface area and body streamlining, respectively (see Pabst, Rommel, and McLellan, Chapter 2, this volume). A third type of drag, wave drag, results from surface waves generated when the swimmer moves on or near the air–water interface. Hertel (1966) measured the changes in drag for a dolphin-shaped model towed on and below the water surface. Near the water surface, drag was four to five times higher than when the model was towed submerged at the identical speed (Fig. 5-6). An increase in drag was observed until the model was placed at least three body diameters below the water surface. Similar results have been reported for towed seals and sea otters (Williams and Kooyman 1985, Williams 1989); at comparable speeds body drag was consistently higher for the animals towed on the water surface than for the same subject submerged (see Fig. 5-5). Clearly, wave drag plays a dominant role in establishing the total body drag of surface swimmers. In view of this, the practice of removing body hair to achieve a more streamlined body in human swimmers undoubtedly provides more of a psychological or perceptual boost than a hydrodynamic benefit.

Two strategies used by marine mammals to avoid prohibitively high levels of drag are abstinence from high velocity movements when on the water surface and maintenance of a submerged body position (Fig. 5-6). Except for the special case of "porpoising" (see below), aquatic mammals rarely swim at high speed for long periods while near the water surface. Sea otters provide a good example of the interplay between body drag and swimming speed. These mammals routinely use three different modes of swimming depending on their behavior. When eating prey, nursing young, or in the initial stages of escape, the otter swims ventral side up on the water surface using alternate or simultaneous strokes by the hind paws. Slow travel over short distances is conducted ventral side down on the water surface using both hind paws for propulsion. Submerged swimming involves dorsoventral undulation of the caudal half of the body. The particular swimming mode chosen will depend on the desired speed of travel. When swimming slowly the sea otter remains on the water surface, but to travel quickly the otter avoids high drag by submerging (Williams 1989). Analogous to the gait change of terrestrial mammals, the switch from surface to submerged swimming by sea otters occurs at approximately 0.8 m/sec. Likewise, the routine cruising speeds of many pinnipeds and cetaceans appear to

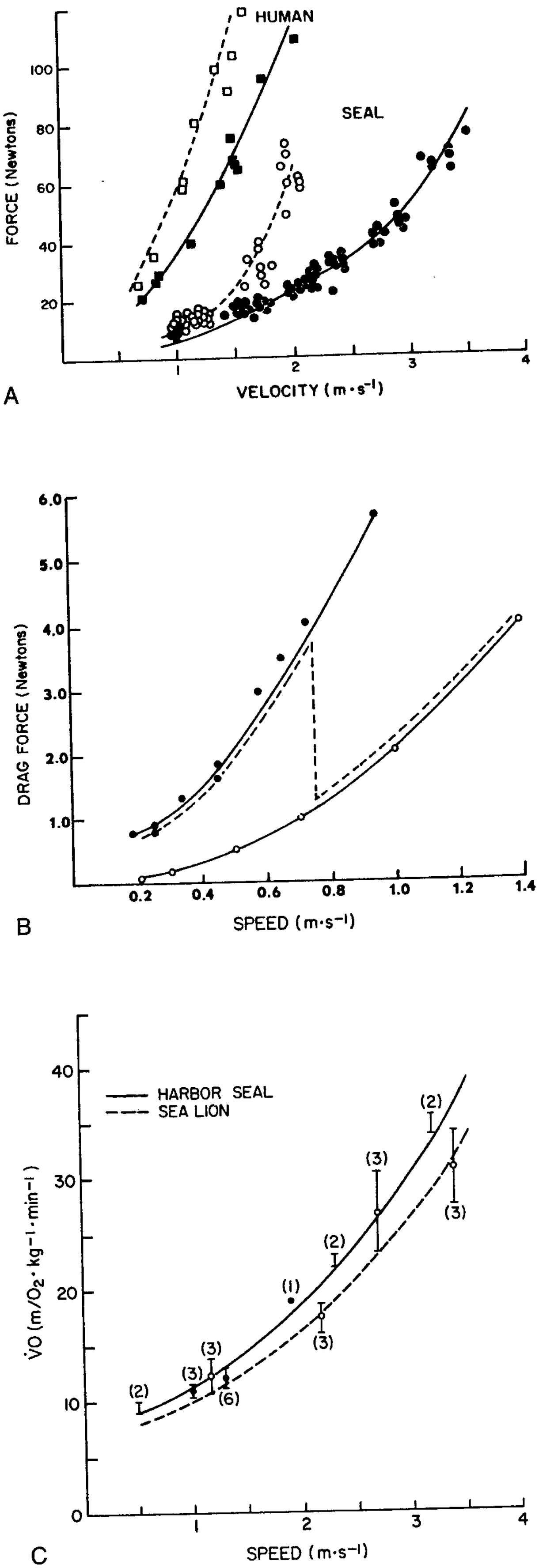


Figure 5-5. Total body drag of harbor seals (submerged = closed circles; surface = open circles) and humans (submerged = closed squares; surface = open squares) (A) and sea otters (submerged = open circles; surface = closed circles) (B) towed at different velocities through seawater. Surface (dashed lines) and submerged (solid lines) body positions are shown for each subject. The dashed line in (B) represents the body drag encountered by a sea otter based on preferred surface and submerged swimming speeds. Graphs are reprinted from Williams and Kooyman (1985) and Williams (1989). (C) The relationship for oxygen consumption in relation to swimming speed for seals and sea lions. Note the similar curvilinear relations for both parameters (drag and oxygen consumption) in relation to speed. (Numbers in parenthese represent number of animals.)

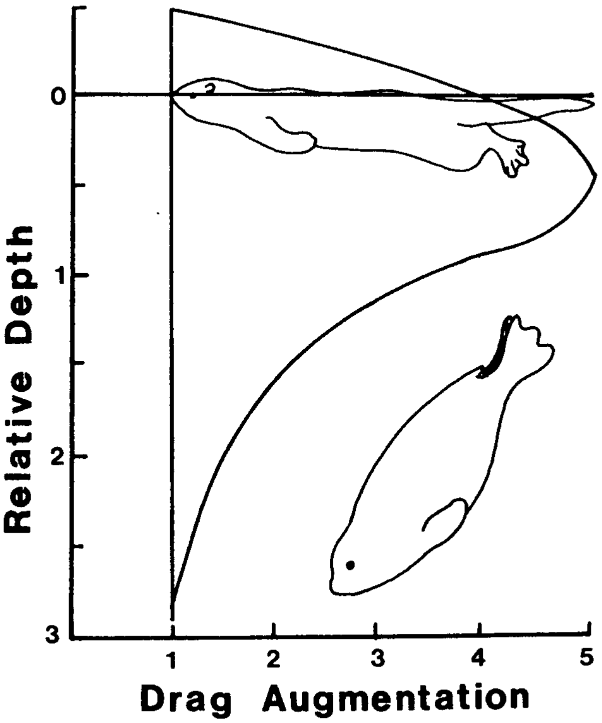


Figure 5-6. The augmentation in body drag in relation to relative depth of the swimmer. The horizontal line can be considered the water surface. Relative depth refers to body diameter of the swimmer. (The sources of data used in this figure are provided in the text.)

be dictated by the relationships between body drag, energetic cost, and velocity.

A submerged swimming position while providing a hydrodynamic benefit to the marine mammal conflicts with the physiological demand to be at the water surface to breathe. A compromise involves the diving response of marine mammals. It is difficult to determine whether the hydrodynamic demands of high-speed swimming or the energetic benefits of being able to forage over a greater range of the water column led to the enhanced breath-holding capabilities of marine mammals. Regardless, marine mammals, by virtue of their adaptations for diving, can swim submerged for prolonged periods and reduce the hydrodynamic and energetic burdens encountered by surface swimmers.

ENERGETIC COST OF SWIMMING. The energetics of swimming in marine mammals reflect the exponential increase in drag that occurs with locomotor speed (see Fig. 5-5). Metabolic rates have been measured for gray seals (*Halichoerus grypus*) (Fedak 1986), harbor seals (Davis et al. 1985), California sea lions (Kruse 1975, Feldkamp 1987), northern fur seals (Feldkamp et al. 1989), and bottlenose dolphins (Williams et al. 1993) swimming over a wide range of speeds. Unlike many terrestrial mammals in which oxygen consumption generally increases linearly with running speed (Taylor et al. 1987), marine mammals often show a curvilinear increase in oxygen consumption with swimming speed. As a result of the nonlinear relationship between energetic effort and speed, the physiological demands associated with swimming at routine speeds may be remarkably low for marine mammals. Bottlenose dolphins provide one example. The metabolic rate, heart rate, respiration rate, and levels of blood lactate of these cetaceans swimming at 2.0 m/sec show only small increases from the values of resting animals (Williams et al. 1993). Compare this with the high respiratory frequency and obvious state of fatigue of the Olympic swimmers after their gold medal sprints at the same swimming speed.

The cost of transport (COT) provides a way to compare the energetic efficiency of locomotion in different animals. The COT is defined as the metabolic cost of moving a unit mass a unit distance (Schmidt-Neilsen 1979), and is calculated by dividing the mass-specific metabolic rate of the animal by its locomotor velocity (VO_2/velocity). The resulting units, mL $O_2 \cdot kg^{-1} \cdot m^{-1}$ can be converted to energy units (joules per kilogram per meter). These are analogous to the gas mileage rating of automobiles. For animal systems we speak of liters per mile or kilometer rather than miles per gallon. The minimum COT indicates the velocity used by the swimmer to travel the greatest distance for the lowest energetic input. The minimum COT occurs in the mid-range of routine swimming speeds and is within the trough of a U-shaped curve that relates COT to swimming speed (Fig. 5-7).

Comparing different types of mammalian swimmers, we find that the minimum COT of aquatic mammals falls into two separate categories, the marine mammals and the semiaquatic mammals (Fig. 5-8). One allometric expression describes total transport costs in relation to body mass for swimming marine mammals ranging in size from 21 to 15,000 kg:

$$\mathrm{COT} = 7.94\mathrm{Mass}^{-0.28},$$

where COT is in joules $\cdot$ $kg^{-1} \cdot m^{-1}$ and mass is in kilograms (Williams 1999). This relationship includes otariid and phocid seals, large and small odontocetes, and a mysticete whale. A second allometric equation that includes muskrats, minks, humans, and surface-swimming sea otters describes the COT of semiaquatic mammals. This relationship,

$$\mathrm{COT} = 23.9\mathrm{Mass}^{-0.15},$$

where COT is in joules $\cdot$ $kg^{-1} \cdot m^{-1}$ and mass is in kilogram, roughly parallels the regressions for marine mammals and for fish (Williams 1989). However, COT is consistently higher for the surface swimming species. Several factors, in-

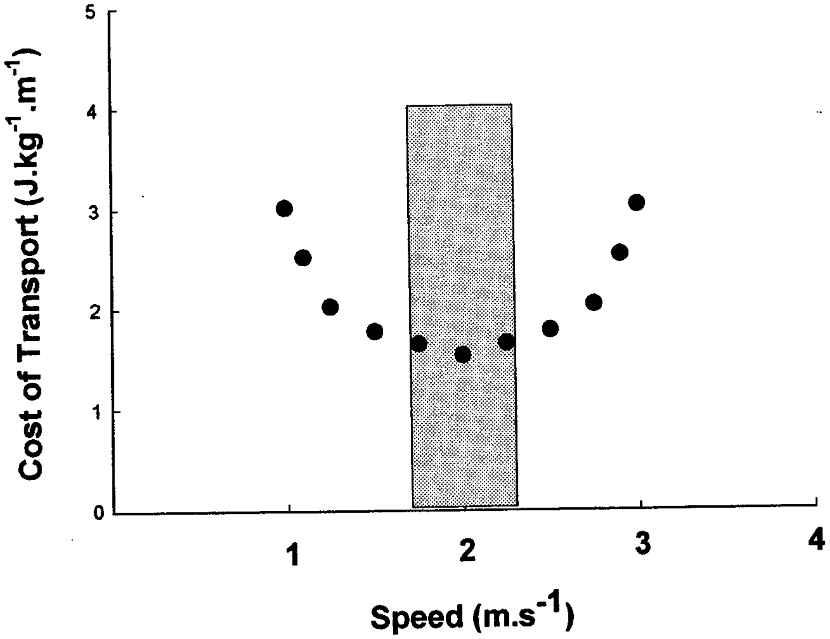


Figure 5-7. The cost of transport (COT) in relation to swimming speed in bottlenose dolphins. The dotted curve was calculated from the values of oxygen consumption determined for animals swimming next to a boat. The shaded area denotes the preferred swimming speeds of wild dolphins in coastal regions. (Reprinted from Williams et al. 1996.)

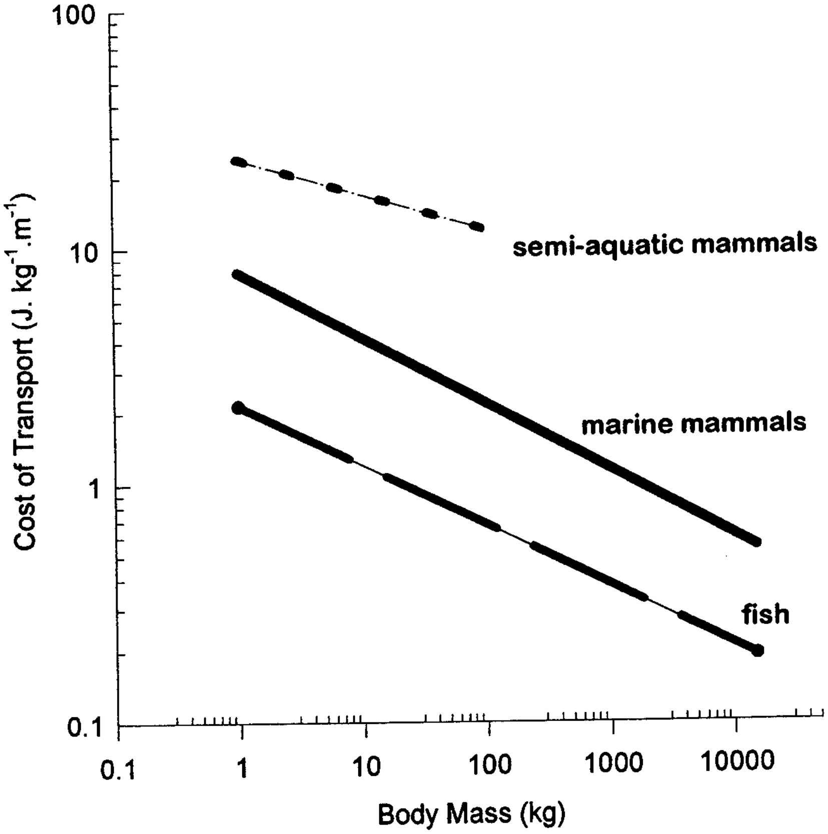


Figure 5-8. Allometric relationships for the minimum COT for swimming vertebrates. The upper dashed line denotes the best fit regression for surface swimmers and includes data for mink, muskrats, and humans. The lower dashed line represents the best fit regression and extrapolation for swimming salmonid fish. The solid line between is the allometric regression for marine mammals ranging in size from a 21-kg juvenile sea lion to a 15,000-kg gray whale.

cluding total hydrodynamic drag, propulsive efficiency, and high maintenance costs, may explain the comparatively high COT of semiaquatic animals. As discussed above, surface-swimming mammals must expend energy to overcome the augmentation in body drag associated with surface wave generation. In addition, semiaquatic mammals typically use paddling modes of swimming rather than the more cost-efficient lift-based propulsion typical of marine mammals (Fish 1993). As a result, the COTs of semiaquatic mammals are 9 to 23 times higher than those predicted for similarly sized fishes, whereas the COTs of marine mammals are only 2 to 5 times higher than such predictions.

Nonetheless, the cost per stroke may not be exceptionally low for marine mammals in comparison to semiaquatic mammals. Figure 5-9 compares the stroking costs for a human performing the front crawl to a dolphin using dorsoventral movements of the flukes to push against a force platform. The remarkable feature of the dolphin's performance is not the animal's metabolic input per se but the amount of work that can be performed for that input. A metabolic input of 60 mL O_2 per stroke allows the human to generate 15 kg of thrust, compared to nearly 100 kg by the dolphin. Differences in efficiency between the different styles of propulsion undoubtedly account in part for different levels of performance (Fish 1993). In addition, the dolphin may be able to take advantage of unique elastic characteristics of the skin and blubber and an arrangement of tendons to generate high levels of thrust for relatively little energetic input (Pabst, Rommel, and McLellan, Chapter 2, this volume).

REDUCING THE ENERGETIC COST OF SWIMMING: MARINE MAMMAL TRICKS. Marine mammals often seem to be in the process of finding the path of least resistance, that is, the most cost-effective way of moving through the marine environment. One relatively simple strategy is to use a submerged mode of swimming. We have already seen that moving under water imparts a hydrodynamic advantage to the swimmer. It also results in a significant physiological benefit.

The ability to swim submerged for sustained periods is an important adaptation for aquatic locomotion in mammals. Marine mammals, by virtue of their physiological responses to diving (i.e., utilization of on-board oxygen stores, bradycardia, and redistribution of blood flow; see Elsner, Chapter 3, this volume) can take advantage of the lower costs associated with submerged swimming. Aquatic species capable of both surface and subsurface modes of swimming (penguins and sea otters) demonstrate the energetic advantage of moving underwater. At 0.8 m/sec the oxygen consumption of sea otters swimming submerged is more than 40% lower than for surface swimming at the same speed (Williams 1989). Little blue penguins (*Eudyptula minor*) show a 40% reduction in COT when changing to a submerged mode of swimming (Baudinette and Gill 1985). In sea otters the COT for surface swimming is more than 12 times the predicted value for a salmonid fish of equal size. This is reduced to six times the predicted fish value when the otter switches to a submerged swimming mode. In view of this, it is little wonder that many marine mammals at sea, whether migrating or moving between prey patches, spend more than 90% of their time below the water surface.

Despite the advantages of remaining submerged, marine mammals must periodically come to the water surface to breathe. Usually, surface intervals are short, comprising less than 1 sec for dolphins and sea lions (Hui 1989). Surface intervals for swimming harbor seals are somewhat longer at 3 to 5 sec depending on swimming speed (Williams et al. 1991). The phocids may take several breaths during this period in contrast to the single breath taken with each surfacing by otariids and cetaceans. The differences in breathing patterns probably reflect morphological differences in lung structure for the different groups of marine mammals. Specifically,

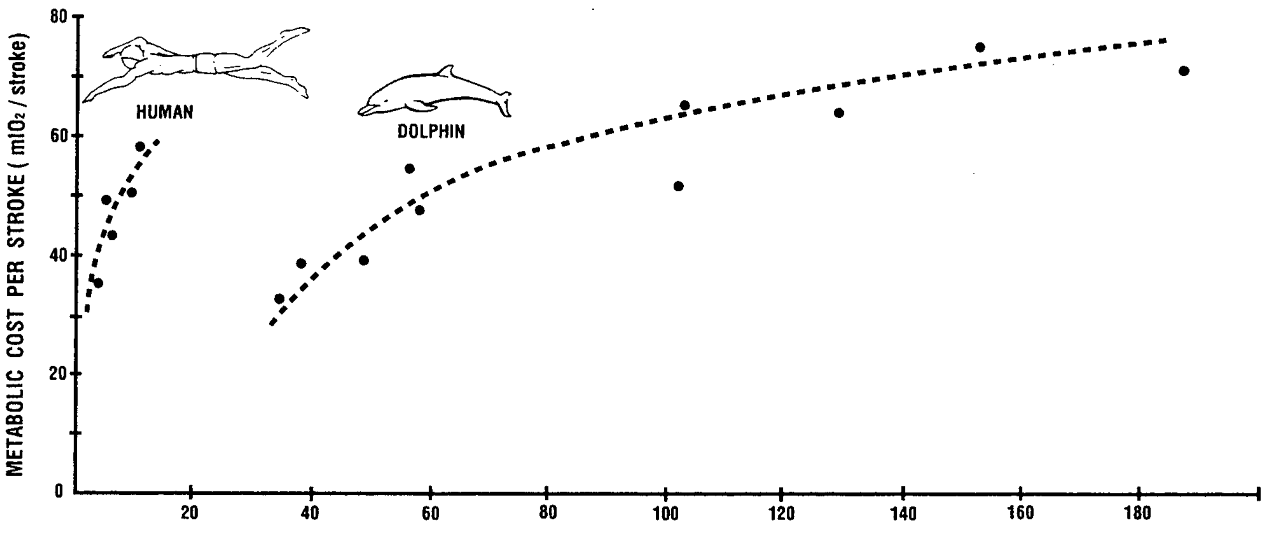


Figure 5-9. The energetic cost per stroke in relation to load for dolphins and humans. Values for dolphins were obtained from animals swimming against a force platform (Williams et al. 1993). Human athletes used swimming strokes to push off submerged force transducers in a pool. (Toussaint 1990.)

cartilaginous reinforcement of the otariid and cetacean lung supports high flow rates of air at low lung volumes during expiration (Drabek and Kooyman 1984). As a result, oxygen loading during the surface interval may be shorter for these animals than for phocid seals and perhaps other marine mammals.

Dolphins also demonstrate a novel solution to the problem of high surface drag; they simply leave the water in a maneuver appropriately termed porpoising. Au and Weihs (1980) and Blake (1983) have constructed theoretical models that predict the cost of swimming on the water surface, swimming submerged, and leaping by dolphins. It is always energetically cheaper to swim submerged at a depth greater than three times body diameter. At low speeds the energetic effort of leaping is greater than that needed to overcome drag encountered on the water surface, and the dolphins should theoretically remain in the water. However, with increasing rates of travel surface wave drag becomes prohibitively expensive. When swimming faster than the calculated transition or crossover speed, the dolphin should take to the air as it surfaces to breathe. To date, these theories have not been tested with actively swimming dolphins. Complicating factors in these tests will be individual and species-specific variations in aptitude and behavioral propensity for leaping.

Wave-riding is another behavioral strategy for reducing the energetic cost of high-speed travel in marine mammals. This behavior is routinely observed from aboard ship when wild dolphins seek the bow and stern wakes of vessels and appear to surf alongside with no apparent tail movements (Scholander 1959). Variations include riding the wake of larger whales, surfing on large wind waves (Woodcock and McBride 1951, Caldwell and Fields 1959), and drifting on currents (Würsig et al. 1985). The energetic benefit of this behavior was investigated for bottlenose dolphins trained by the U.S. Navy to match their speed to that of a moving boat. When the dolphins positioned themselves in the boat's wake their COT at 3.8 m/sec was nearly identical to that of the same animals freely swimming outside of the wake at only 2.1 m/sec. In other words, wave-riding behavior allowed the dolphins to move almost twice as fast for the same energetic cost. In addition, heart rate, respiration rate, and levels of postexercise blood lactate were reduced (Williams et al. 1992). Except for the occasional surfing sea lion or harbor seal, it is unusual to observe species other than small cetaceans take advantage of this energy-saving behavior.

Diving marine mammals may use several other behavioral strategies to reduce activity costs during the descent and ascent portion of their dives. Changes in buoyancy, interrupted modes of swimming, and prolonged periods of gliding during descent affect the energetic cost of a dive (Williams et al. 1996). Because marine mammals must limit their period of submergence to account for on-board oxygen reserves (Kooyman 1981), behavioral adjustments that reduce energetic costs potentially increase the duration of the dive. High-speed ascents and descents, and elevated thermoregulatory costs act to increase the total energetic demand of a dive and significantly reduce the time available for foraging. Conversely, the use of burst-and-glide modes of swimming increases allowable foraging time. The energetic implications of these observations for the actively foraging marine mammal are addressed in detail when we discuss at-sea metabolic rates.

The Cost of Growth and Reproduction

For growth and reproduction to occur an animal must acquire energy and nutrients in excess of that required to support maintenance functions. These additional energy costs vary with the species of marine mammal, sex, and reproductive pattern (for a general overview of all marine mammal reproductive biology, see Boyd, Lockyer, and Marsh, Chapter 6, this volume). An excellent example is the difference in reproductive costs for males and females. In pinnipeds, polar bears, sea otters, and probably mysticetes and sirenians, the cost of reproduction in males is limited to the cost of finding and maintaining access to estrous females. Evolution favors a pattern of energy expenditure that maximizes reproductive success in males. This may be demonstrated by monitoring changes in body mass or body composition of males over the breeding season (Anderson and Fedak 1985, Deutsch et al. 1990, Boyd and Duck 1991, Bartsh et al. 1992, Coltman 1996). Interestingly, the costs associated with reproduction in aquatic and terrestrially breeding males are quite similar when normalized for differences in body mass (Coltman 1996; Fig. 5-10). Larger body size is preferred in terrestrially breeding male pinnipeds as it both confers an advantage in fighting (Haley et al. 1994, Anderson and Fedak 1985). In addition, larger animals can fast longer because they have a lower mass-specific metabolic rate than smaller animals; this allows the male to maintain terrestrial territories longer (Bartholomew 1970). In species that compete for females in the water, we find that the males are comparatively smaller than the species that breed on land. For the aquatic breeders, underwater agility is more important than large size when competing for mates. It is also possible for the male to leave on short foraging trips and then return to the breeding area. Even among these aquatic breeders, large males have an advantage over small males. By reducing the number of foraging trips, large males can establish an advantage over small males in terms of time available for competing for females (Coltman 1996).

The cost of reproduction for females can be broken down into the energy requirements for gestation (the cost of pro-

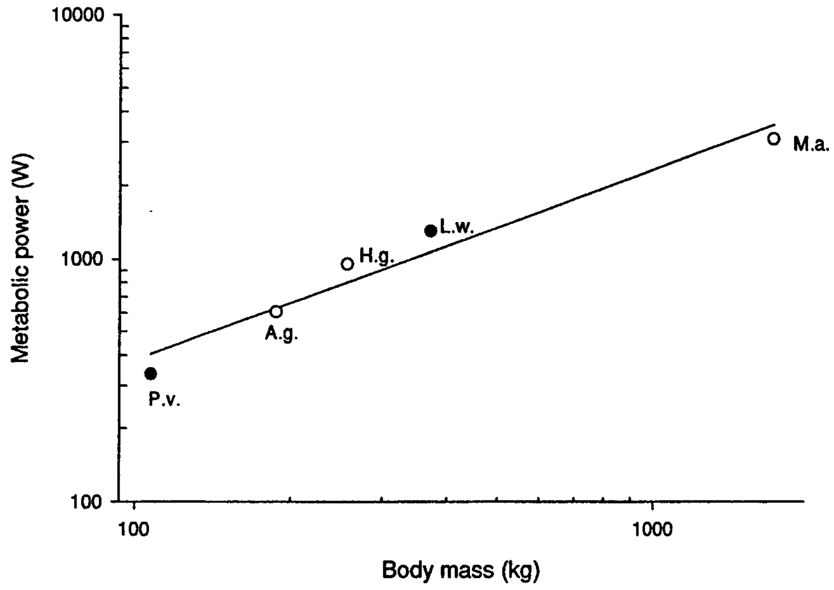


Figure 5-10. Metabolic power of breeding male pinnipeds is shown relative to body mass. Solid circles are for males with aquatic territories and open circles for males with terrestrial territories. Data are for *A.g.*, Antarctic fur seals (Boyd and Duck 1991); *P.v.*, harbor seals (Coltman 1996); *H.g.*, gray seals (Anderson and Fedak 1985); *L.w.*, Weddell seal (Bartsh et al. 1992); and *M.a.*, northern elephant seals (Deutsch et al. 1990). The line represents the least squares linear regression of all data ($R^2 = 0.95$, where $W = 10.45(kg)^{0.78}$).

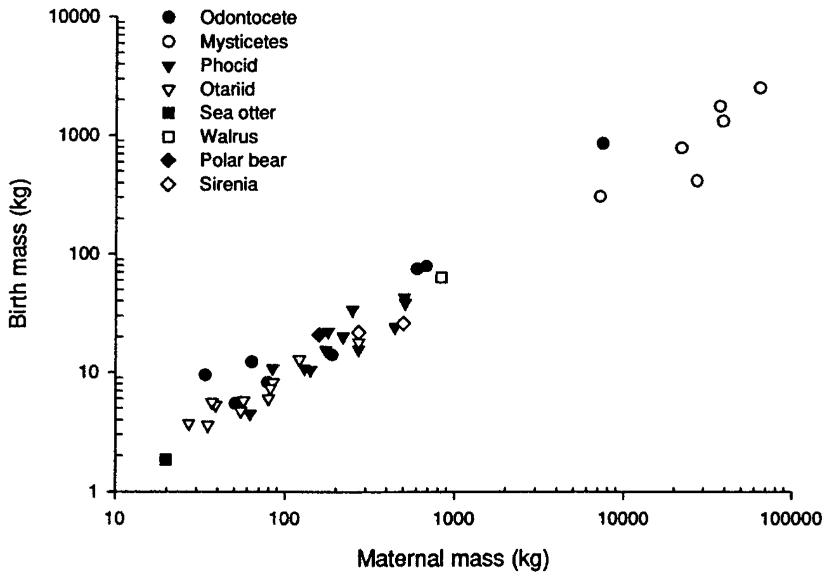


Figure 5-11. Birth mass plotted in relation to maternal mass for marine mammals. Data from Brodie 1971; Rice and Wolman 1971; Lockyer 1977, 1978, 1981a,b, 1984, 1995; Hartman 1979; Best 1982; Fay 1982; Best and da Silva 1984; Christen 1984; Kasuya and Marsh 1984; Perrin and Henderson 1984; Kovacs and Lavigne 1986, 1992b; Ramsay and Stirling 1988; Read 1990; Riedman and Estes 1990; Bowen 1991; Costa 1991a; Kretzman et al. 1991; Derocher et al. 1993; Koski et al. 1993; Martin and Rothery 1993; Perrin and Hohn 1994; Marsh 1995; Marmontel 1995; Rathbun et al. 1995; Reyes and Van Waerebeek 1995.

ducing a fetus) and for lactation (the cost of nursing young until weaning). These costs depend on the rate and intensity of investment by the mother. In marine mammals the pattern of maternal investment is quite variable with profound effects on both the energetics of the individual animal and the species. Maternal investment patterns of marine mammals vary among the taxonomic groups and in many ways dictate life history characteristics.

Although no direct measurements on the cost of gestation are available for marine mammals, investigations of terrestrial eutherians suggests that the cost of producing a fetus is insignificant relative to the costs associated with lactation (Millar 1977). Fetal mass at birth relative to maternal mass can be used as a relative index of the cost of gestation. Among marine mammals, we find that there are no striking differences in birth mass relative to maternal mass (Fig. 5-11). This is not surprising in view of the relatively low energetic cost of producing a fetus. Conversely, lactation strategies vary markedly with maternal body mass among different marine mammal groups (Fig. 5-12). Phocid seals and mysticete whales have significantly shorter lactation durations for their body size than do other marine mammals. The remaining groups are surprisingly similar. A comparison of growth rate as a function of maternal mass indicates that the shorter lactation duration of phocids is compensated for by an increase in growth rate (Fig. 5-13). Otariids, polar bears, sea otters, walruses, and odontocetes have remarkably similar growth rate patterns relative to maternal mass (Boyd, Lockyer, and Marsh, Chapter 6, this volume).

Comparisons of maternal investment patterns must consider differences in the behavior and metabolic rates of the mother and her young. For example, although phocid pups are weaned at an early age, they are not truly nutritionally independent at that time; they rely on maternally derived energy, stored as blubber, for weeks or months after weaning. In contrast, other marine mammals, such as otariids, sea otters, and odontocete cetaceans, wean their offspring much later. As a result, the young are not as reliant on energy reserves stored before weaning. A longer lactation period requires that more energy be supplied to the young in support of its maintenance metabolism. Perhaps for this reason, many marine mammal young begin to feed before weaning with the result that the animal is nutritionally independent when weaning does occur. Obviously, a longer development period requires greater maternal investment.

Longer lactation periods allow the young to acquire a greater proportion of lean tissue growth (Costa 1991a). Growth in phocid young primarily takes the form of adipose tissue with proportionately little growth in lean tissue. Otariids show proportionately greater increases in lean mass during the lactation interval (Bryden 1968; Worthy and Lavigne 1983b; Ortiz et al. 1984; Oftedal et al. 1987; Arnould et al.

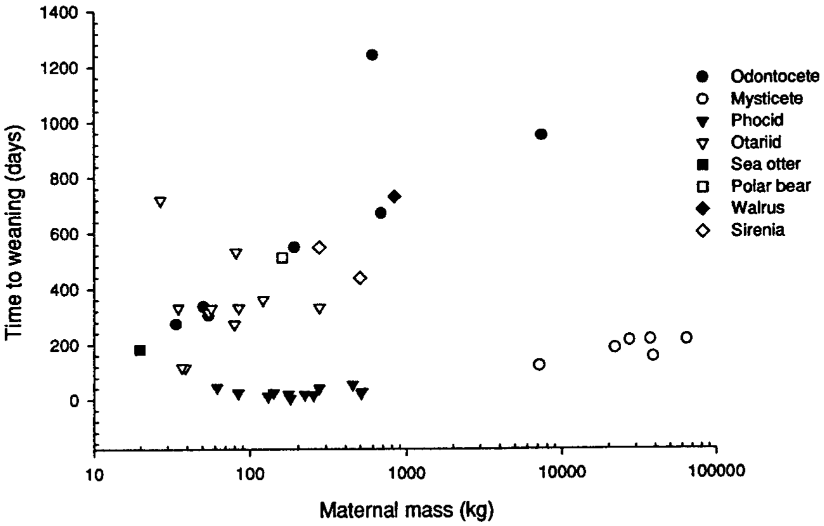


Figure 5-12. Time to weaning plotted as a function of maternal mass for marine mammals. Lactation durations of phocid seals and mysticete whales are shorter than all other marine mammals. Data from Brodie 1971; Rice and Wolman 1971; Lockyer 1977, 1978, 1981a,b, 1984, 1995; Hartman 1979; Best 1982; Fay 1982; Best and da Silva 1984; Kasuya and Marsh 1984; Perrin and Henderson 1984; Kovacs and Lavigne 1986, 1992b; Ramsay and Stirling 1988; Read 1990; Riedman and Estes 1990; Bowen 1991; Costa 1991a; Kretzman et al. 1991; Derochere et al. 1993; Koski et al. 1993; Martin and Rothery 1993; Perrin and Hohn 1994; Marsh 1995; Marmontel 1995; Rathbun et al. 1995; Reyes and Van Waerebeek 1995.

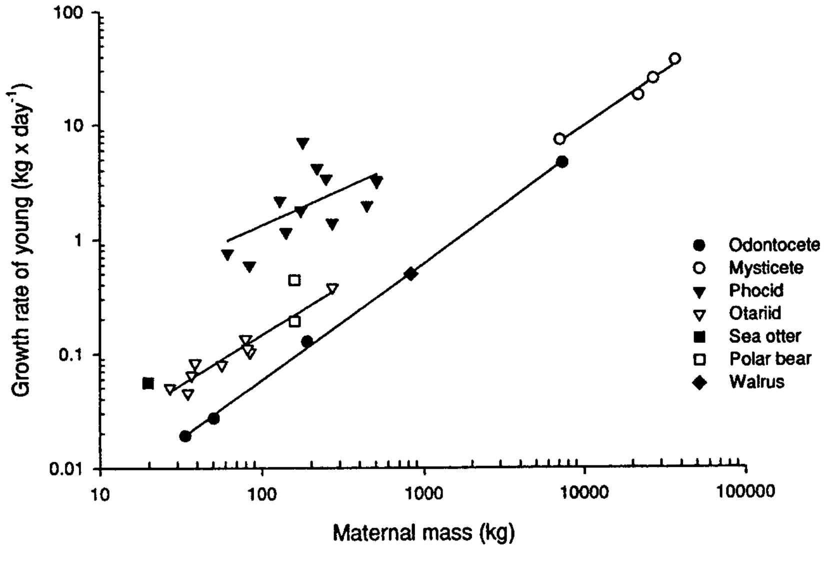


Figure 5-13. Growth rate of suckling marine mammals as a function of maternal mass. Lines represent least squares regressions for each taxonomic group. Data are from Brodie 1971; Rice and Wolman 1971; Lockyer 1977, 1978, 1981a,b, 1984, 1995; Best 1982; Fay 1982; Best and da Silva 1984; Christen 1984; Kasuya and Marsh 1984; Perrin and Henderson 1984; Kovacs and Lavigne 1986, 1992b; Ramsay and Stirling 1988; Read 1990; Riedman and Estes 1990; Bowen 1991; Costa 1991a; Kretzman et al. 1991; Derocher et al. 1993; Koski et al. 1993; Martin and Rothery 1993; Perrin and Hohn 1994; Reyes and Van Waerebeek 1995.

1996a,b). The longer dependency period of otariid pups requires a greater utilization of energy for maintenance functions. This diverts energy from growth and requires that otariid mothers provide more energy for an equivalent relative mass at weaning.

The relationship between lactation duration and weaning mass is well illustrated by a comparison of northern elephant seals and northern fur seals. Northern elephant seal pups are born at 7.5% of maternal mass, are nursed over a 28-day lactation interval, and are weaned at 26% of maternal mass. After weaning, pups remain on the beach fasting for 2.5 months (Reiter et al. 1978) and then go to sea to feed after losing approximately 30% of their mass at weaning (Kretzmann et al. 1993). Pups are not nutritionally independent until they are at least 3.5 months of age (Ortiz et al. 1978) and by this time weigh 18% of maternal mass. Northern fur seal mothers suckle their pups over a 4-month period and wean them at 35% of maternal mass. At or near weaning, northern fur seal pups have begun to feed and may be considered nutritionally independent. Consequently, northern fur seal pups may be proportionately larger at nutritional independence than northern elephant seal pups. In addition to physiological factors, the duration of lactation may be dictated by the habitat of the marine mammals. This is especially apparent for phocids (Kovacs and Lavigne 1986) and is an important factor that permits this group to breed on ice (Stirling 1975, 1983). The shortest lactation interval and fastest growth rates for pups occur in pack ice breeding seals such as hooded (*Cystophora cristata*) and harp seals. The longest lactation intervals are found in species that breed on fast ice such as Weddell (*Leptonychotes weddellii*) and ringed seals. Because fast ice is firmly attached to the shore, it is quite stable. Conversely, pack ice is a very unstable breeding substrate and can disappear at any time. The shortened lactation interval of pack ice seals ensures that the pup is weaned before the break up of the pack (Bowen et al. 1985, Bowen 1991). Island-breeding phocids, including elephant and gray seals, that feed far offshore show an intermediate pattern. These animals may not be able to feed during the lactation period because the food resource is too distant. As a result, there would be a significant advantage in concentrating the investment interval to reduce metabolic overhead (Fedak and Anderson 1982). By shortening the lactation period, a higher proportion of stored maternal resources can go into milk production rather than maternal maintenance metabolism (see below). The comparatively long lactation interval of Weddell seals, ringed seals, and island-breeding harbor seals allows these species to augment their maternal reserves by feeding because prey are nearby (Testa et al. 1989, Boness et al. 1994, Boness and Bowen 1996). With the proximity of food, feeding trips may be shortened during lactation. This results in a concomitant decrease in pressure on the female to shorten the investment interval and reduce metabolic overhead. It is unlikely that such short-duration feeding trips could supply sufficient energy to support the rapid growth rates of phocid pups. Most of the energy and materials supplied to the pup are still derived from maternal body reserves.

BODY SIZE AND MATERNAL RESOURCES: THE ROLE OF MATERNAL OVERHEAD. Fasting during lactation is a unique component of the life history pattern of marine mammals. With the exception of bears, no other mammal is capable of producing milk without feeding. By undertaking this energetic challenge, mysticetes and pinnipeds are able to temporally and spatially separate feeding from breeding. Separation of lactation from feeding allows mysticete whales to feed in the highly productive polar regions of the world's oceans, but retain the thermal advantage of breeding in the calm tropical regions. Migrating to warmer waters for parturition reduces the thermal demands on the newborn calf and provides additional energetic advantages for the mother.

Among pinnipeds, the separation of feeding from lactation allows terrestrial parturition and pup rearing and at-sea foraging by the female. Most phocids store what is required for the entire lactation period, whereas all otariids feed during lactation (Bonner 1984, Kovacs and Lavigne 1986, Oftedal et al. 1987, Costa 1991a, Kovacs and Lavigne 1992a). Phocid mothers remain on or near the rookery continuously from the birth of their pups until they are weaned; milk is produced from body reserves stored before parturition. Although some phocids feed during lactation, most of the maternal investment is derived from body stores. Weaning is abrupt and occurs after a minimum of 4 days of nursing in hooded seals to a maximum of 6 to 7 weeks in Weddell or monk seals (*Monachus* spp.). In contrast, otariid mothers remain with their pups for approximately 1 week after parturition and then periodically go to sea to feed. The pup is suckled intermittently between foraging trips (Bonner 1984).

The ability of a marine mammal female to fast while providing milk to her offspring is related to the size of her energy and nutrients reserves and the rate at which she uses them. When food resources are far from the breeding grounds, as may occur for some phocids and large mysticete whales, the optimal solution is to maximize the amount of energy and nutrients provided to the young and to minimize the amount expended on the mother. Fedak and Anderson (1982) used the term "metabolic overhead" to define the amount of energy a female pinniped expends on herself while ashore suckling her pup (Fig. 5-14). However, this concept can be applied to all marine mammals that lactate while fasting.

One mechanism for reducing metabolic overhead is to attain large body size. This results from the relationship between maintenance metabolism, which scales as $mass^{0.75}$, and fat stores, which scale as $mass^{1.0}$ (Fig. 5-15) (Calder 1984, Millar and Hickling 1990, Lindstedt and Boyce 1985). These relationships demonstrate that as body size increases, energy reserves increase proportionately faster with mass than maintenance metabolism. This implies that larger females have a greater ability to provision their young from stored body reserves than smaller females.

The relationship between metabolic overhead, milk production, and lactation duration has been modeled using data from northern elephant seals (Costa 1993a). The total amount of energy available for maternal investment was assumed to be constant, and metabolic overhead was calculated for each lactation duration. Milk production was calculated as the proportion of maternal resources remaining after the cost of the metabolic overhead was met for a given lactation duration. Not surprisingly, the net amount of energy used for maternal maintenance increases with increasing lactation duration; a concomitant decrease in the energy available for milk production is observed. This model indicates that a shorter lactation period is advantageous because the mother can devote more of her energy stores to milk production than to maternal maintenance.

As stated above, a large female should have a lower metabolic overhead than a small female. If we allow our model to include variations in maternal mass as well as lactation duration, we find that metabolic overhead can be minimized by either increasing body mass or reducing the duration of lactation. The strategy for small phocid seals (i.e., ringed seals, harbor seals) is to maintain short lactation periods or to feed during lactation. Large phocids, such as elephant seals or extremely large mysticete whales, are able to maintain longer lactation intervals as metabolic overhead is minimal because of their large size (Fig. 5-16).

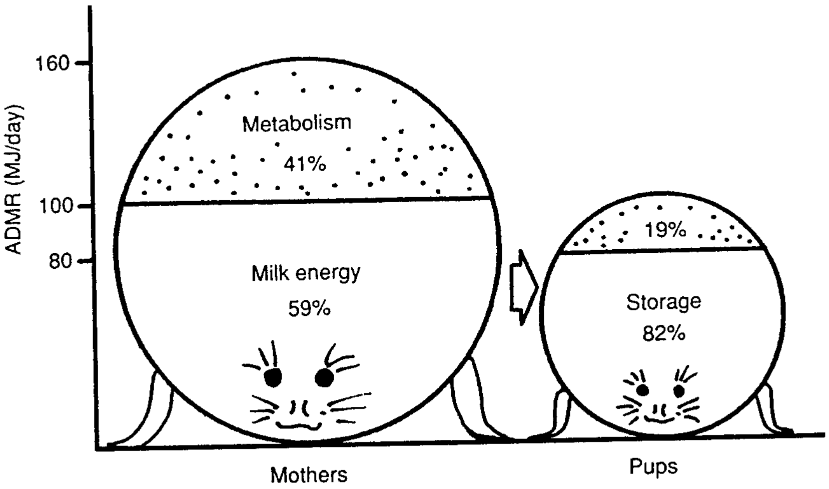


Figure 5-14. Total energy budget of a typical northern elephant seal mother graphically divided between the energy expended on her maintenance metabolism and that contained in the milk fed to the pup. The pup's total energy budget is divided between energy storage and that used for maintenance metabolism. (Figure drawn by A. C. Huntley from data in Costa et al. 1986.)

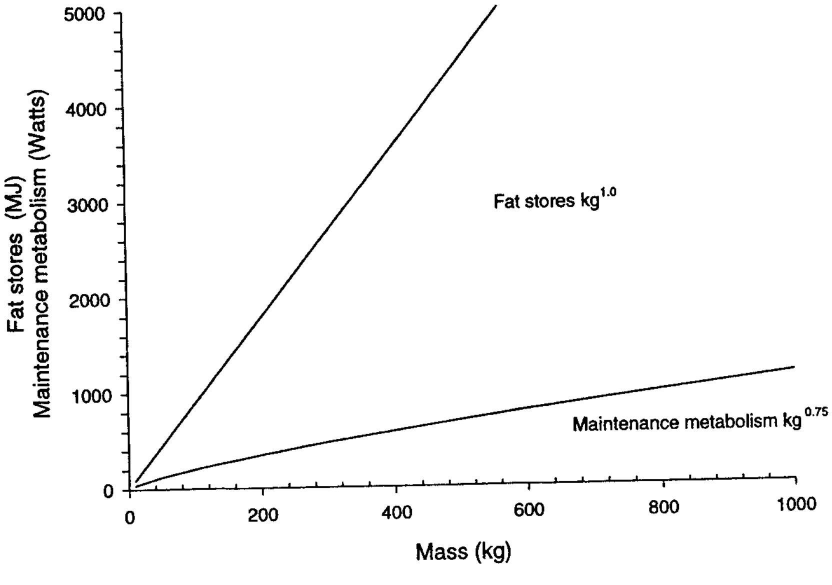


Figure 5-15. The theoretical relationship between fasting metabolic rate and adipose tissue content plotted as a function of maternal body mass for a typical phocid female. Fasting metabolic rate scales with body mass raised to the 0.75 power, whereas fat stores scale linearly with body mass.

Although a comparison of maternal investment strategies for different marine mammal groups would be interesting, there is little information available for species other than pinnipeds. Cetaceans, sirenians, sea otters, and polar bears may spend their entire lives at sea. Therefore, measurements of milk intake, feeding rates during lactation, or other features of reproductive investment are not possible for comparison at this time.

MATERNAL METABOLISM. Variation in maternal metabolism, at least within the otariids, appears to be linked to ambient temperature. Galapagos fur seal females in the warm equatorial environment exhibit fasting metabolic rates on land that are only 1.1 times the predicted basal metabolic rate (Costa and Trillmich 1988). In contrast, northern and Antarctic fur seals (*Arctocephalus gazella*) inhabiting the cold subpolar environment exhibit metabolic rates 3.4 times predicted levels (Costa and Trillmich 1988). Decreases in an animal's onshore metabolism may be achieved by a reduction in activity as observed for phocids and otariids or by periodic breathing as occurs in phocids (Costa et al. 1986, Costa and Trillmich 1988).

The ability to store energy also differs between otariids and phocids. The available data indicate that phocid mothers store significantly more fat than otariids. Values range from 24.5% fat for harbor seals to 47% for harp seals. In comparison, Galapagos, northern, and Antarctic fur seals, and California and Australian sea lions (*Neophoca cinerea*) show 26%, 22%, 19%, 13%, and 8.3% body fat, respectively. With the exception of the Galapagos fur seal, these otariids appear to maintain fasting onshore metabolic rates similar to those of phocids when corrected for body mass (Fig. 5-17) (Costa 1991a, Bowen et al. 1992, Fedak et al. 1996). Overall, the ability of phocid seals to store most if not all of the maternal energy and nutrients before arriving onshore may be attributed to (1) large body size, (2) low metabolic overhead, and (3) greater lipid reserves (Costa 1991a, 1993a).

ENERGY INVESTMENT AND TRIP DURATION. Many phocids fast throughout the lactation interval, whereas otariid females spend 0.5 to 14 days at sea foraging between visits to suckle the pup on the rookery (Gentry and Holt 1986). How do otariid mothers modify the timing and patterning of energy and nutrient investment to accommodate for such different trip durations? If we plot trip duration and milk energy consumed by the pup (normalized for maternal mass$^{0.75}$), we find that otariid mothers making short feeding trips provide their pups with less milk energy than mothers that make long trips (Fig. 5-18). Such a pattern is consistent with the predictions of central place foraging theory (Orians and Pearson 1977), which predicts the optimal behavior of animals foraging at varying distances from a central place, such as a nest or rookery. For example, when foraging a long distance from the rookery, a parent should make few trips of long duration and return with a greater quantity of energy per trip. In contrast, parents feeding close to the

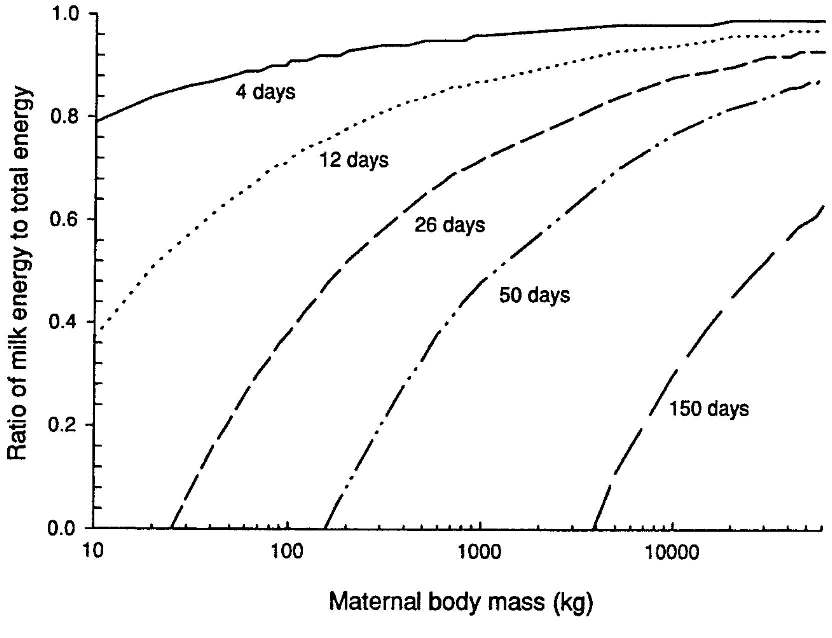


Figure 5-16. The importance of maternal mass and lactation duration on the proportion of total maternal energy available for milk production is detailed in this figure. Lactation durations and maternal mass vary from small phocids (4 days, 100 kg) to mysticete whales (150 days, 60,000 kg). Notice that for small animals it is critical to have a short lactation interval. However, longer lactation intervals are possible with large body size.

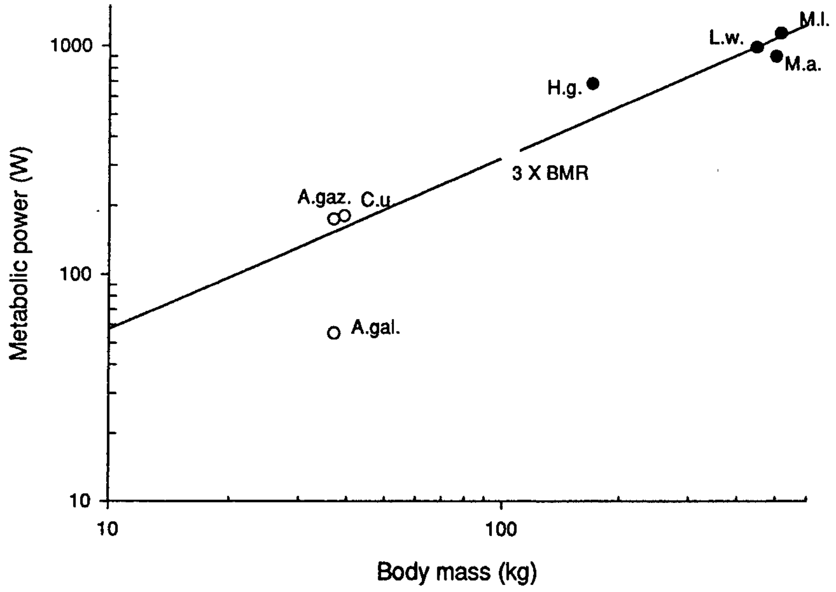


Figure 5-17. Fasting metabolic rate plotted as a function of maternal body mass for four phocids (solid symbols) and three otariids (open symbols). Data were collected using labeled water methodologies (Costa and Gentry 1986, northern fur seals (*C.u.*); Costa and Trillmich 1988, Antarctic fur seals (*A. gaz.*), Galapagos fur seals (*A. gal.*); Costa et al. 1986, northern elephant seals (*M.a.*); Fedak et al. 1996, southern elephant seals (*Mirounga leonina* [*M.l.*]). Measurements derived from mass change data are for gray seals (*H.g.*) Fedak and Anderson 1982 and, Weddell seals (*L.w.*) Tedman and Green 1987. The solid line represents three times the basal metabolic rate for a terrestrial animal of equal size (Kleiber 1975).

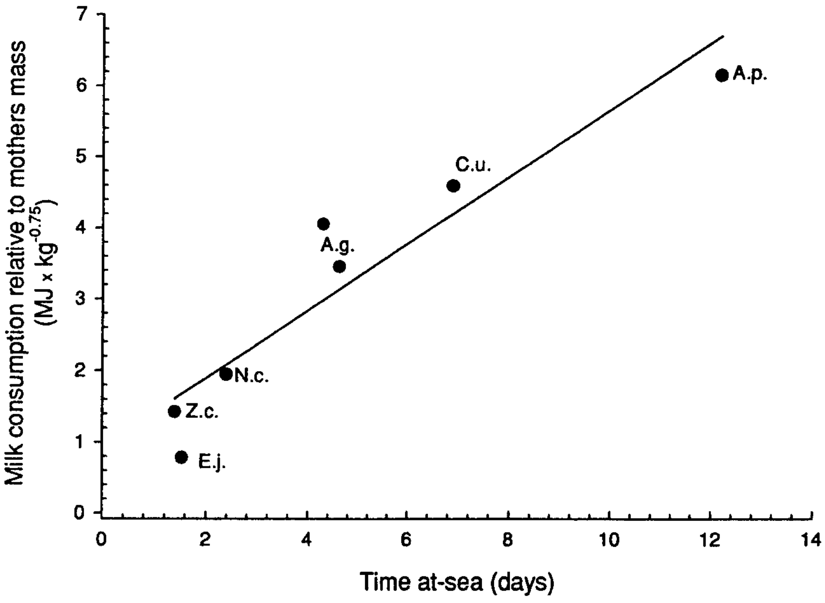


Figure 5-18. Total milk energy consumed by pups per shore visit normalized by dividing by maternal metabolic mass$^{0.75}$ and plotted in relation to the amount of time the mother typically spends at sea feeding before the shore visit. Symbols are for *E.j.*, Steller sea lion (Higgins et al. 1988), *Z.c.*, California sea lion (Oftedal et al. 1987), *A.g.*, Antarctic fur seal (two points, one each from Costa 1991b, Arnould and Boyd 1995a,b), *N.c.*, Australian sea lion (Costa 1991b), *C.u.*, northern fur seal (Costa and Gentry 1986), *A.p.*, Juan Fernández fur seal (Acuña 1995). The line represents the least squares linear regression where milk consumption (MJ × kg$^{-0.75}$) = 8.91(days)$^{0.47}$, $R^2 = 0.883$).

rookery (near-shore) should make many short trips, with a comparatively lower energy return per trip. Otariids, such as the Steller sea lion (*Eumetopias jubatus*), make trips of relatively short duration (approximately 36 hr), feed near shore, and travel short distances to the feeding grounds (Higgins et al. 1988). Northern fur seals feed up to 100 km offshore and make trips of 7 days duration (Loughlin et al. 1987). As predicted by the model, Steller sea lions deliver considerably smaller amounts of milk energy (0.8 MJ × kg$^{-0.75}$) per visit to their pup than northern fur seals (4.6 MJ × kg$^{-0.75}$). A similar pattern is observed for fur seal species. Inshore feeding species (i.e., Galapagos fur seals) forage for less than 24 hr between shore visits to suckle their pups (Trillmich et al. 1986). Offshore feeding species, such as Antarctic, northern, and Juan Fernández fur seals (*Arctocephalus philippii*) may spend anywhere from 4 to 12 days at sea foraging (Doidge et al. 1986, Gentry and Holt 1986, Acuña 1995).

Lactating northern fur seal females consume 80% more food than nonlactating females (Perez and Mooney 1986). Such elevated rates of food intake can only be sustained in the highly productive water characteristic of upwelling environments. Therefore, the absence of a truly tropical otariid may be related to these high reproductive demands and the lower productivity of warmer waters. (The Galapagos fur seal and sea lion are not considered truly tropical species as they exist in a highly productive equatorial upwelling region; Maxwell 1974.)

Optimization of foraging behavior is also observed for phocids. Island-breeding species represent an extreme example of an offshore feeder that uses highly dispersed or distant prey resources and makes as few trips as possible per reproductive event. Elephant seals and gray seals have separated feeding from onshore lactation. The reproductive pattern of these phocids is less constrained by the time it takes to travel and exploit distant prey, which may allow utilization of a more dispersed or patchy food resource. By spreading the acquisition of prey energy required for lactation over many months at sea, northern elephant seal females need to increase their daily food intake by only an estimated 12% to cover the entire cost of milk production and maternal metabolism if we assume that the food energy needed for lactation is consumed over the entire trip to sea (Costa et al. 1986).

In comparison to otariids, phocids may have a reproductive pattern that is better suited for dealing with dispersed or unpredictable prey or prey that is located at great distances from the rookery. The ability of some phocids to forage over long distances is influenced by reducing the importance of feeding during lactation. However, fasting during lactation places a limit on the duration of investment and this limits the total amount of energy that a phocid mother can invest in her pup (Costa 1991a).

What enables otariids and phocids to forage at sea for such variable intervals and yet supply their pups with an appropriate amount of energy? The answer is that the lactation process enables pinnipeds to concentrate the material fed to the young with some independence from prey quality (Pond 1977), or distance or time spent away from the rookery. It is well documented that marine mammals in general, and pinnipeds in particular, produce milk extremely high in lipid (Pilson and Kelly 1962; Bonner 1984; Oftedal et al. 1987, 1996). Although the milk reflects the basic constituents consumed by the mother, she can process, concentrate, or use stored reserves in the production of milk. For example, some species feed on fish, whereas others feed on fish or squid. Yet all of these species provision their offspring with milk of significantly greater energy density than the prey consumed (Fig. 5-19).

Increasing the lipid content of milk to modify the energy density of milk has a disadvantage. The high energy density of pinniped milk is achieved by increasing the lipid content with a reciprocal decrease in water content but no corresponding change in protein content. Therefore, the protein-to-energy ratio of pinniped milk is lowest in the most energy-dense milk. Young may be provided with more than sufficient energy to fuel metabolism but may be limited in their ability to grow due to the reduced protein intake. This is especially important in species that have shortened lactation intervals like hooded seals. In such species, pups receive similar amounts of total energy in smaller quantities of milk. Because the protein content of the milk is independent of lactation duration, these

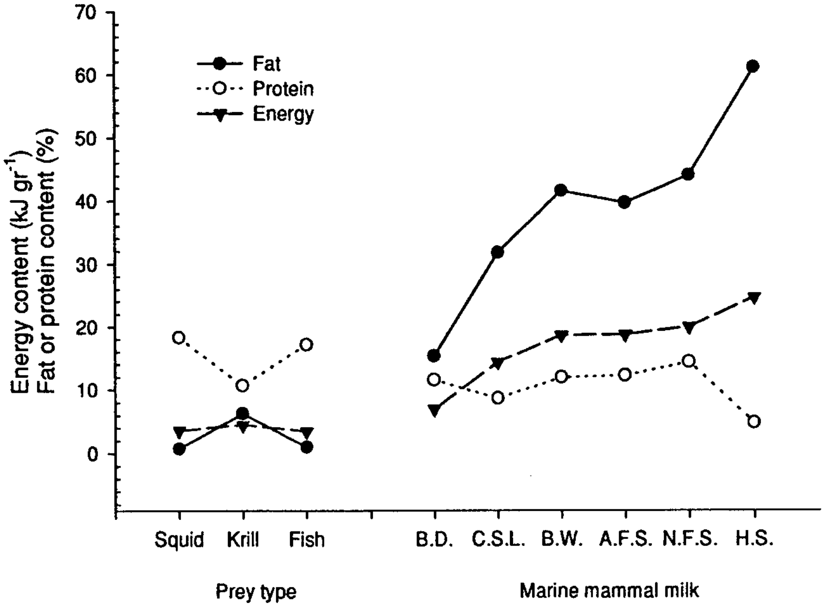


Figure 5-19. The energy density and protein content of squid, notothaenid fish, krill, and milk of bottlenose dolphins (*B.D.*), California sea lions (*C.S.L.*), blue whale (*B.W.*), Antarctic fur seal (*A.F.S.*), northern fur seal (*N.F.S.*), and hooded seal (*H.S.*). Data on squid and fish are from Perez and Mooney (1986); krill from Clarke (1980); California sea lions from Oftedal et al. (1987); Antarctic fur seal, Costa et al. (1985); bottlenose dolphins, D. P. Costa, unpubl.; blue whale, Lockyer (1984); and hoded seals, Oftedal et al. (1988).

pups get less total protein. This constraint can be seen by the fact that most of the postnatal growth of phocid seals is due to the accumulation of adipose tissue stored as blubber with little growth in lean tissue (Bryden 1968, Worthy and Lavigne 1983a, Costa et al. 1986, Oftedal et al. 1987). Thus, northern elephant and harp seal pups are born almost without fat but are composed of approximately 50% lipid at weaning (Worthy and Lavigne 1983a,b; Ortiz et al. 1984).

VARIATION IN MILK COMPOSITION. A consistent adaptation among all marine mammals is that they produce a high-fat and, therefore, energy-rich milk (Fig. 5-20). With a few exceptions, most terrestrial animals produce milk that is fairly low in fat; cows and humans produce milk that contains 4% and 8% milk fat, respectively. The variation in milk fat among marine mammals is correlated with the duration of time that the mother and calf are together. For example, the highest milk fat contents are observed in pinnipeds, particularly phocid seals that spend only a few days to weeks with their pups. A fat, energy-rich milk allows the mother to transfer high levels of energy in a very short period of time. Hooded seals are most impressive with a 4-day lactation interval and a milk fat of 65% lipid (Oftedal et al. 1988). In view of this, it is not surprising that marine mammals with the highest growth rates produce milk with the highest lipid content (Fig. 5-21). However, there is considerable variation in the milk fat content of marine mammals with unexceptional growth rates.

Variations in milk fat content, particularly among otariids, appear to be related to maternal attendance patterns (Costa 1991a). Lipid and, therefore, energy content of the milk of otariids increases with trip duration (Trillmich and Lechner 1986). Correlations between milk fat content and trip duration are complicated by the fact that otariid females with short trip durations are low latitude species and those with long trip durations are high latitude species. High latitude environments are highly seasonal and may force shorter lactation periods than low latitude species (Oftedal et al. 1987).

Ecological Implications of Energy Flow

Field Metabolic Rates

In the preceding sections, we discussed the various components that comprise the energy costs associated with exis-

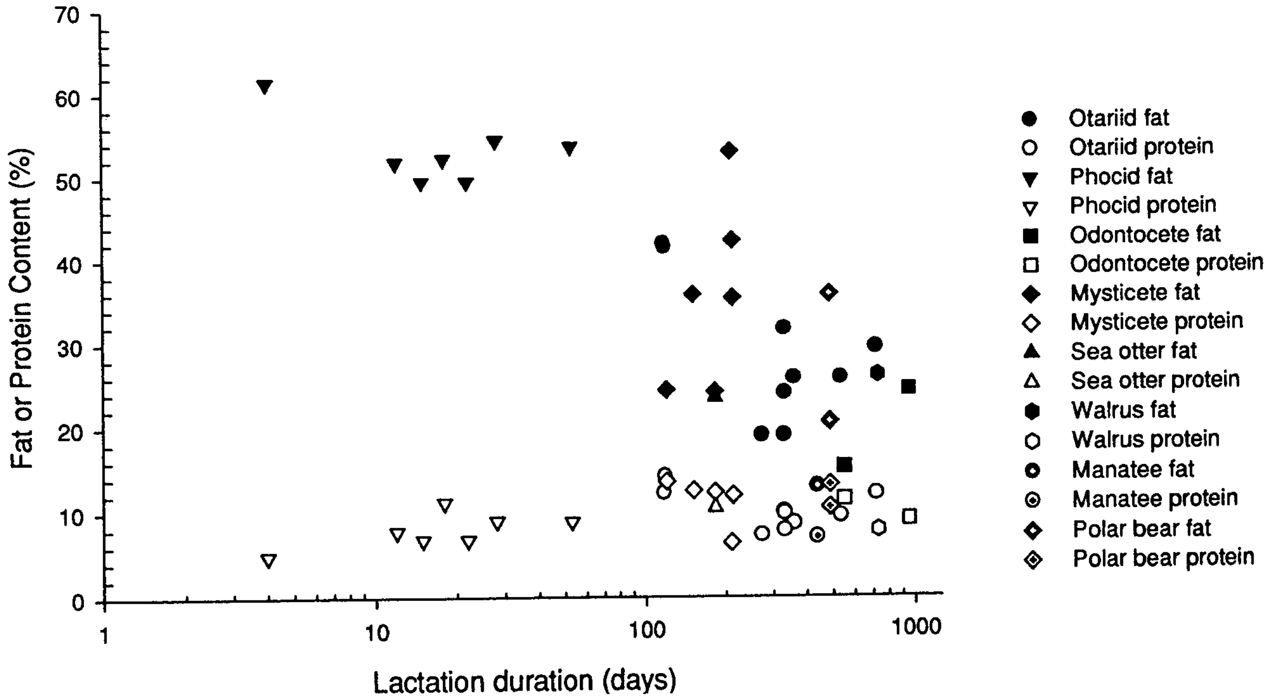


Figure 5-20. Fat (solid symbols) and protein (open symbols) content (%) for marine mammal milk as a function of lactation duration. Data are from Rice and Wolman 1971; Lockyer 1977, 1978, 1981a,b, 1984, 1995; Best 1982; Fay 1982; Best and da Silva 1984; Ramsay and Stirling 1988; Read 1990; Riedman and Estes 1990; Bowen 1991; Costa 1991a; Kretzman et al. 1991; Derocher et al. 1993; Acuña 1995; Marsh 1995; Marmontel 1995; Rathbun et al. 1995.

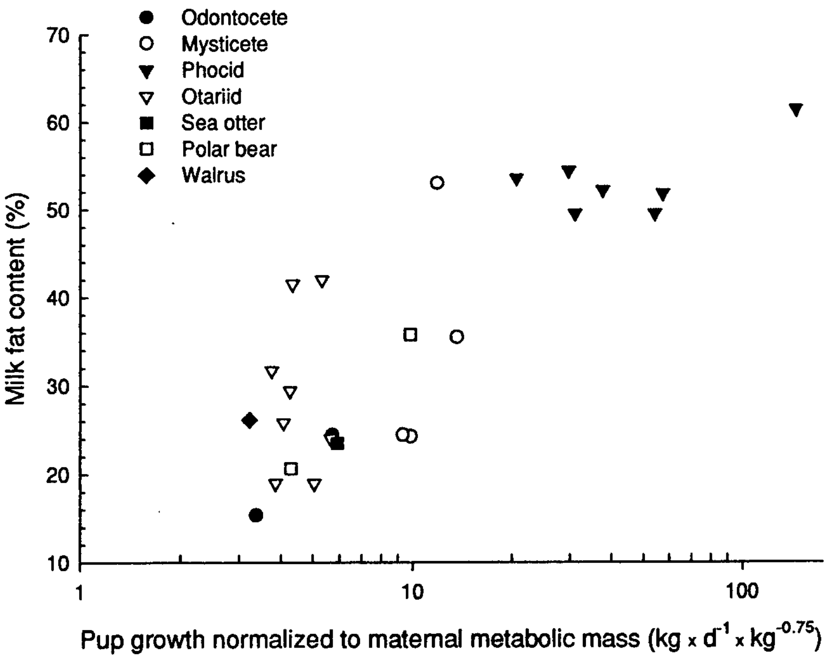


Figure 5-21. Milk fat content of marine mammal milk plotted in relation to the growth rate of the young corrected to maternal metabolic mass ($kg^{0.75}$). Data are from Rice and Wolman 1971; Lockyer 1977, 1978, 1981a,b, 1984, 1995; Best 1982; Fay 1982; Best and da Silva 1984; Ramsay and Stirling 1988; Read 1990; Riedman and Estes 1990; Bowen 1991; Costa 1991a; Kretzman et al. 1991; Derocher et al. 1993; Acuña 1995.

tence for a marine mammal. Although these individual components provide an understanding of energetic adaptations, it is the sum of all of these activities and processes that determine the overall energetic cost of existence, commonly referred to as field metabolic rate. In the following sections, we examine the overall energy budget of marine mammals and how it varies with foraging ecology for different marine mammal species.

A number of approaches have been used to study the energetics of animals at sea. One approach, time budget analysis, sums the daily metabolic costs associated with various activities. Field observations of behavior are coupled with metabolic rate measurements made in captivity. Other methods rely on predictive relationships between physiological variables and metabolic rate. For example, metabolic costs can be assessed indirectly by measurement of changes in body mass and composition (Fedak and Anderson 1987), variations in heart rate or ventilation rate (Sumich 1983; Dolphin 1987a,b; Butler et al. 1992, 1995; Williams et al. 1993), or dilution of isotopically labeled water (Costa 1987, Anderson et al. 1993). Metabolic rates calculated from heart rate or ventilation rate assume that the level of oxygen consumed is directly related to each breath or heart beat. Estimates of metabolic rate from changes in body mass may be based on direct measurements or estimated changes in the relative proportion of fat and protein of an animal. Isotopic measurements of metabolic rate rely on changes in the concentration of two isotopes of water within body compartments. In this method, two isotopes of water are given to the animal orally or by injection. After equilibration, an initial blood sample is taken and the animal is released. After a period of 3 to 10 days, a final blood sample is taken. The metabolic rate is then determined from the change in concentration of the two isotopes in the blood. The first isotope, tritium- or deuterium-labeled water, decreases in the animal's blood as a function of the water exchange through the animal. The second isotope, oxygen-18-labeled water, declines as a function of the animal's water exchange and CO_2 production. The arithmetic difference between the disappearance rate of deuterium- or tritium-labeled water (water only) and oxygen-18-labeled water (water and CO_2) provides an estimate of the animal's rate of CO_2 production, and hence, metabolic rate (Lifson and McClintock 1966, Nagy 1980, Costa 1987).

Field metabolic rates (FMR) provide insight into the energetic strategies used by marine mammals. For example, to determine whether phocids and otariids use different strategies while foraging, we could compare the metabolic rates of each species actively foraging at sea. Comparisons of the metabolic costs associated with pup maintenance while onshore may be assessed by monitoring females while they suckle their pups on the beach. Not surprisingly, there are limited data on field metabolic rates to make such comparisons for marine mammals. The best data exist for pinnipeds and the bottlenose dolphin (Fig. 5-22) and indicate that foraging otariids and bottlenose dolphins expend energy at six times the predicted basal metabolic level (Costa and Gentry

1986; Costa et al. 1989b, 1995). In contrast, the metabolic rate of diving elephant seals is only two to three times the predicted basal rate (D. P. Costa, unpubl.). Metabolic rates of Weddell seals freely diving from a hole in the ice have been determined by indirect calorimetry at a rate of 1.5 to 2 times the predicted basal level (Kooyman et al. 1973, Castellini et al. 1992).

How might differences in field metabolic rate affect the foraging energetics and behavioral strategies of a marine mammal? As air breathers, foraging marine mammals are physiologically constrained by the amount of oxygen they have stored in their tissues and the rate at which this oxygen is used. Although animals can increase the duration of individual dives by using anaerobic metabolism, it is energetically more efficient to rely on aerobic metabolism (Kooyman et al. 1980, 1983; Kooyman 1989; Elsner, Chapter 3, this volume). The maximum time an animal can remain submerged without using anaerobic metabolic pathways is called the aerobic dive limit (ADL) as defined by:

$$\text{ADL} = \text{Total oxygen store (mL } O_2) \text{ / Metabolic rate during dive (mL } O_2 \times \text{min}^{-1})$$

The total oxygen store is represented by the oxygen reserves in the blood, muscle, and lung (Kooyman 1985). The bigger the ADL, the longer a marine mammal can carry out an uninterrupted search or the deeper it can dive. Thus, the foraging capability of an animal is related to the balance between its total oxygen store and its utilization rate as dictated by diving metabolic rate (see Elsner, Chapter 3, this volume).

To understand the relationship between diving metabolism and foraging behavior, the oxygen storage capability of marine mammals must be considered. As a group, phocids have large oxygen stores in comparison to other marine mammals. This suggests that phocids demonstrate the

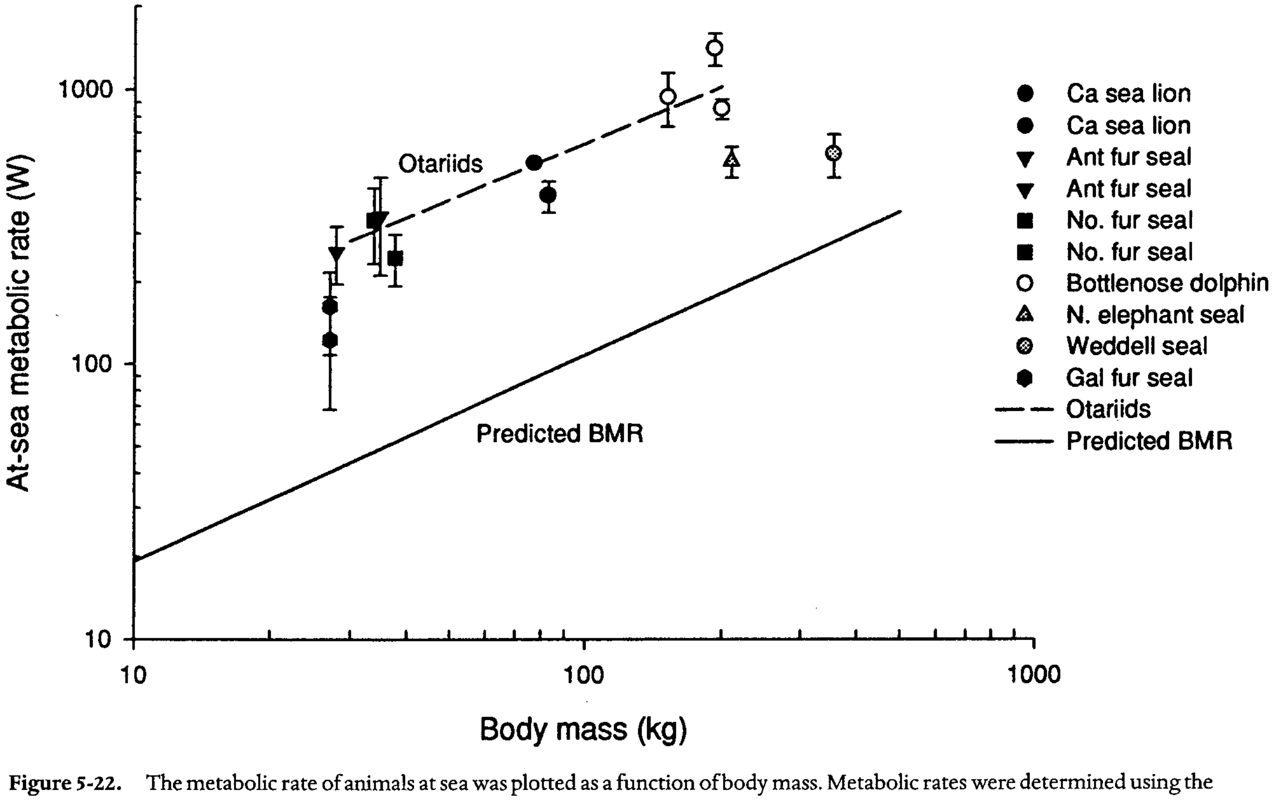


Figure 5-22. The metabolic rate of animals at sea was plotted as a function of body mass. Metabolic rates were determined using the oxygen-18 doubly labeled water method and are from northern fur seals (Costa and Gentry 1986), Antarctic fur seals (Costa et al. 1989a), Australian sea lions (Costa et al. 1989b), California sea lions (Costa et al. 1991), Galapagos fur seals (Trillmich 1990), bottlenose dolphins (Costa et al. 1995), and northern elephant seals (D. P. Costa, unpubl.). Weddell seals were measured using open circuit respirometry on seals diving from an ice hole (Castellini et al. 1992). The solid line represents the predicted basal metabolic rate (BMR) for a terrestrial animal of equal size (Kleiber 1975); the dashed line is the best fit linear regression for the otariids with the exception of the Galapagos fur seal ($r^2 = 0.53$). Error bars represent ± one standard deviation.

greatest diving ability. Small electronic data recorders, which can be attached to marine mammals, allow us to test this prediction by providing information about the diving patterns of marine mammals (Figs. 5-23 and 5-24). These devices record at programmed intervals the animal's depth and swim speed, water temperature, and other parameters. In most cases, data are stored on computer memory chips, and the unit must be recovered to retrieve the information. In some units, the information can be downloaded via a satellite link. However, current technology significantly limits the amount of information that can be obtained from a satellite uplink (Costa 1993b). Data on dive depth and duration obtained with such instruments are summarized in Figures 5-25 and 5-26; these data indicate that phocids and sperm whales are exceptional divers, often displaying long and deep dive patterns, whereas otariids and most cetaceans are shallow, short-duration divers.

The greater diving ability of phocids is not unexpected as they can store more oxygen per kilogram of body mass than otariids or most cetaceans (Kooyman 1989). However, the greater oxygen storage capacity of phocids can only account for a 50% increase in dive duration. From Figure 5-26 we can see that phocid seals can actually dive up to 10 times longer than most other marine mammals. The additional diving ability can be explained by their extremely low metabolism during diving (Castellini et al. 1992, Costa 1993a) compared to the high at-sea metabolic rate typical of otariids (see Fig. 5-22). Using the ADL equation, we can model the relative importance of metabolic rate and oxygen stores to diving ability of a phocid and an otariid (Fig. 5-27). In this model, the ADL for a phocid is calculated from the metabolic rates measured for Weddell seals (1.4 and 2 times basal metabolic rate) and an oxygen storage capacity of 60 mL O_2/kg. We calculated ADL based on an oxygen storage capacity of 40 mL O_2/kg (for otariids), 35 mL O_2/kg (for dolphins), and metabolic rates of 6 times basal metabolic rate determined from measurements of each species' sea metabolism. Although differences among dolphin, otariid, and phocid oxygen storage capacities have a significant effect on ADL, the differences in at-sea metabolism have a greater impact. Figure 5-27 also demonstrates that larger phocids have a greater aerobic dive limit than smaller ones. This is attributable in part to differences in scaling parameters for metabolic rate and total oxygen stores with body mass. Metabolic rate scales to body mass$^{0.75}$, whereas oxygen storage capacity scales to body mass$^{1.0}$ (same pattern in Fig. 5-15). This means that larger mammals have a lower mass-specific metabolism for a relatively constant proportion of oxygen storage capacity (Kooyman et al. 1983, Gentry et al. 1986, Kooyman 1989). All things being equal, large mammals should be able to dive longer and deeper than small ones based simply on body size. Thus, for phocid seals greater diving capability is due to the combined effects of (1) greater oxygen storage capacity, (2) significantly reduced metabolism during diving, and (3) large body size.

The effect of body size on ADL is not as great for otariids or dolphins as it is for phocids and may be attributable to differences in diving metabolism. For marine mammals with a high metabolic rate we find little change in ADL as body mass increases. However, larger body mass does result in a greater absolute demand for food. Small body size, although

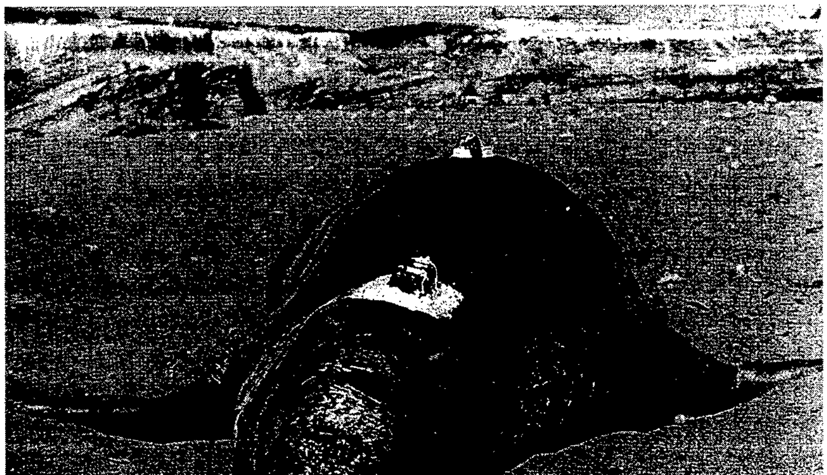


Figure 5-23. A male northern elephant seal male rests on the beach with a satellite-linked transmitter attached to the top of his head and a time-depth recorder attached to the middle of his back. The satellite transmitter only transmits when the animal is at the surface and provides a fix of his location at sea. The time-depth recorder must be recovered to acquire the data.

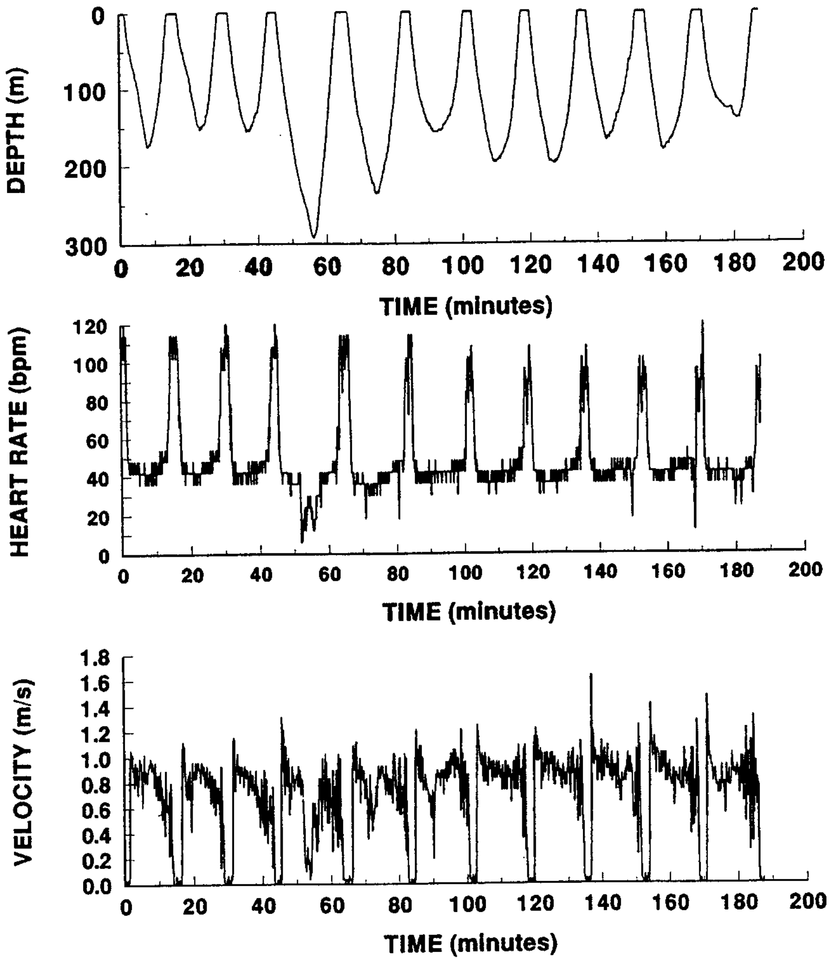


Figure 5-24. An example of the kind of information that can be obtained using archival data loggers. This record included data on time, depth, swim velocity, and heart rate that were obtained from a freely swimming juvenile northern elephant seal. (P. M. Webb, unpubl.)

resulting in a higher mass-specific metabolism, decreases absolute food energy requirements (Peters 1983, Millar and Hickling 1990). An advantage of lower absolute food requirements is that one can sustain oneself on smaller prey patches, which are likely to be more abundant. In terrestrial communities, high-quality food tends to be quite patchy and of lower overall abundance, providing an advantage for the smaller animal. These differences provide important insights into the evolution of optimal body size in marine mammals. If we assume that diving ability is an important component of the life history pattern of phocids, we would expect large body size to be favored because of the benefits of increased diving capability. In contrast, smaller size might be favored in otariids because they gain more from the reductions in absolute energy requirements than they get by minimal increases in dive duration resulting from greater mass.

There are other well-established differences in diving physiology and behavior among phocids, otariids, and small cetaceans. Phocids and monodontids have comparatively higher blood oxygen storage capacities owing to an increased proportion of red blood cells (hematocrit) (Lenfant et al. 1970). However, an elevation in hematocrit increases the blood viscosity and reduces the ability of the blood to optimally transport oxygen (Hedrick et al. 1986; Hedrick and Duffield 1991; Elsner, Chapter 3, this volume). Fortunately, maximum oxygen-carrying capacity is not an issue for phocids and monodontids that are able to maintain low metabolic rates while diving. In addition, behavioral differences among these groups result in differences in the costs of foraging (see Wells, Boness, and Rathbun, Chapter 8, and Bowen and Siniff, Chapter 9, this volume). For example, otariids and delphinids typically travel at the surface porpoising, whereas phocids tend to surface quietly and descend before swimming. The energetic implication of these behaviors has been addressed in the preceding section on activity costs. In general, otariids appear to use a more expensive foraging strategy that is optimal when resources are abundant. Phocids use a comparatively slow, energetically economical foraging pattern. Thus, the otariid life history pattern favors time minimization, whereas that of phocid favors energy minimization.

Differences in the Cost and Efficiency of Foraging

Different diving patterns and energy expenditures undoubtedly affect the ability of pinnipeds to obtain prey and the effi-

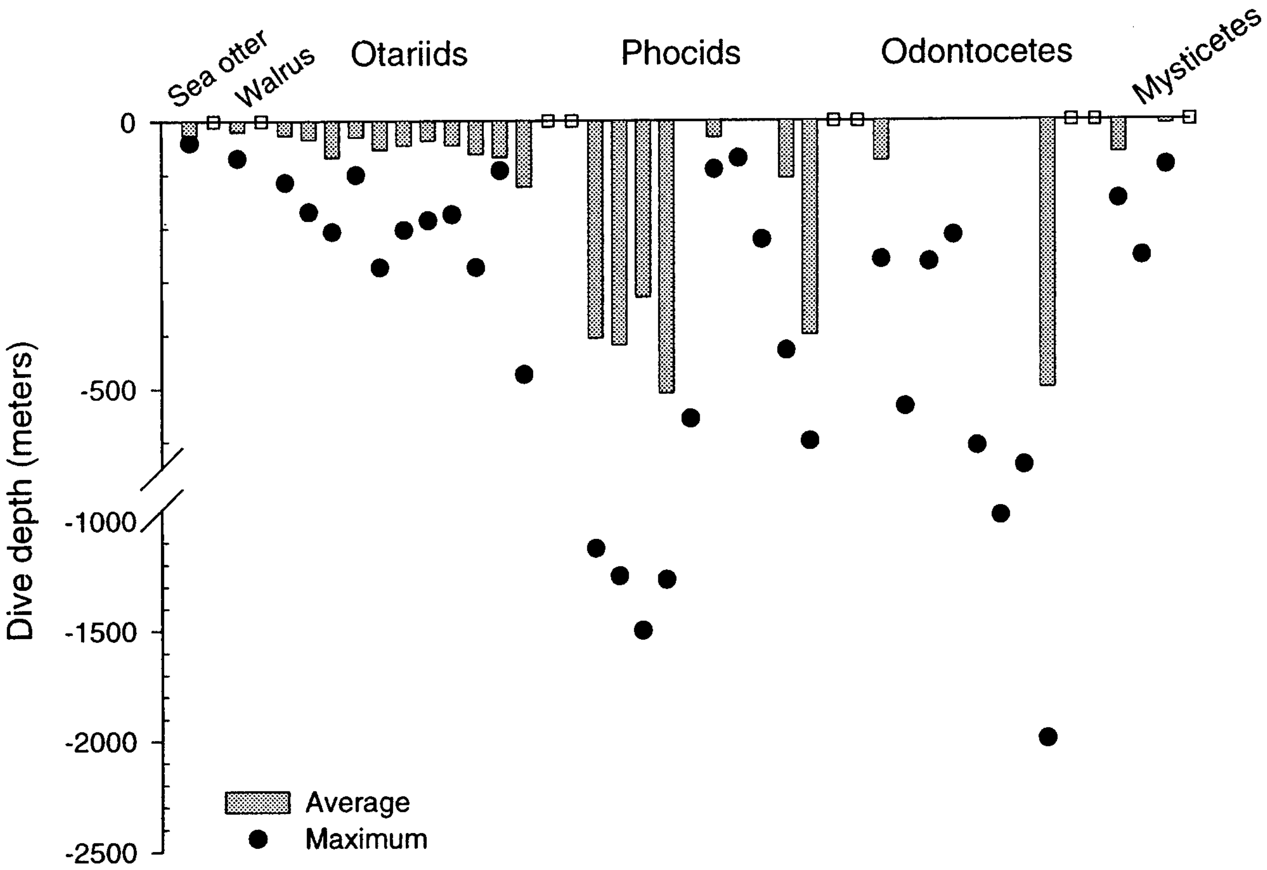


Figure 5-25. Maximum (dots) and where available mean (histogram) diving depth for 32 species of marine mammals. The squares at 0 depth represent breaks between the different taxonomic groups. The data are from left to right: sea otter; walrus: otariids: Galapagos fur seal, South American fur seal (*Arctocephalus australis*), northern fur seal, New Zealand fur seal (*Arctocephalus forsteri*), South African fur seal (*Arctocephalus pusillus pusillus*), Galapagos sea lion, South American sea lion (*Otaria byronia*), California sea lion, Australian sea lion, New Zealand sea lion; phocids: southern elephant seal male, female, northern elephant seal male, female, harbor seal, harp seal, gray seal, ringed seal, crabeater seal (*Lobodon carcinophagus*), Weddell seal; odontocetes: common dolphin (*Delphinus delphis*), bottlenose dolphin, killer whale, Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), pilot whale (*Globicephala* spp.), narwhal (*Monodon monoceros*), beluga whale (*Delphinapterus leucas*), sperm whale; mysticetes: humpback whale (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), northern right whale (*Eubalaena glacialis*). Data are from Kooyman and Andersen 1969, Evans 1974, Kolb and Norris 1982, Gentry et al. 1986, Gales and Mattlin 1997, Ridgway 1986, Dolphin 1987b, Gentry et al. 1987, Le Boeuf et al. 1988, Costa et al. 1989b, Feldkamp et al. 1989, Riedman and Estes 1990, Hindell et al. 1991, Stewart and DeLong 1991, Thompson et al. 1991, Bengtson and Stewart 1992, Castellini et al. 1992, Wartzok et al. 1992, Lydersen and Kovacs 1993, Watkins et al. 1993, Wiig et al. 1993, Heide-Jorgensen and Dietz 1995, Werner and Campagna 1995, Winn et al. 1995.

ciency with which they acquire energy. Dive performance for a sea lion, a fur seal, and an elephant seal are presented in Table 5-3. Although elephant seals obtain more prey energy per dive than either northern fur seals or California sea lions, they take more time to do it, and acquire less energy per unit time. The ratio of energy acquired to energy expended is the same between the sea lion and the elephant seal, but is significantly greater for the fur seal. These data imply that a high metabolic rate may be advantageous in achieving high rates of prey consumption. There is a cost to this strategy, however, in terms of the animal's absolute energy requirements. Although the elephant seal is 10 times larger than the fur seal and four times larger than the sea lion, its absolute energy expenditure is almost identical to both. Despite large size, the absolute energy intake of the elephant seal is equivalent to that of the sea lion and only one quarter that of a fur seal. This

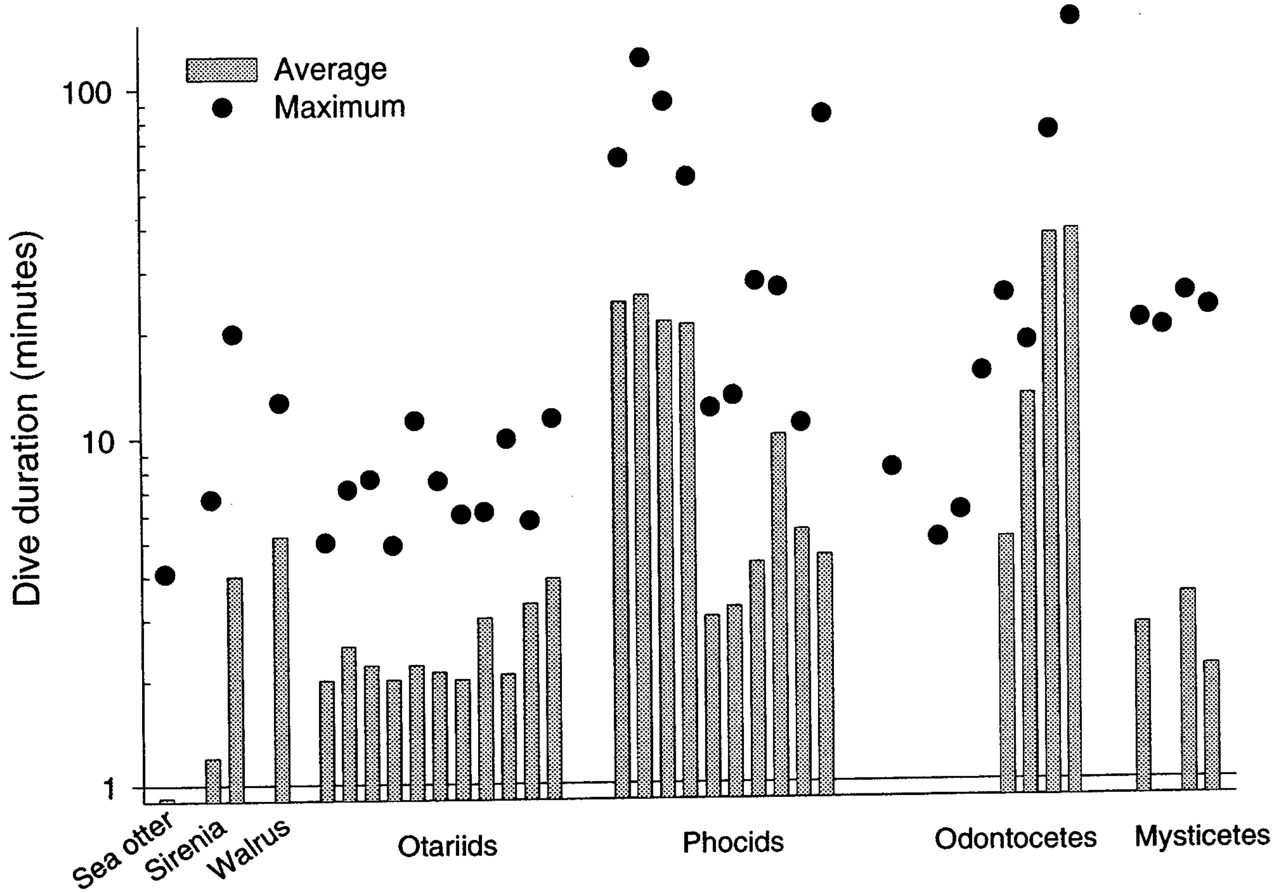


Figure 5-26. Maximum (dots) and where available mean (histogram) diving duration for sirenia: dugong, manatee; otariids: Galapagos fur seal, South American fur seal, northern fur seal, Antarctic fur seal, New Zealand fur seal, South African fur seal, Galapagos sea lion, southern sea lion, California sea lion, Australian sea lion, New Zealand sea lion; phocids: southern elephant seal male, female, northern elephant seal male, female, harbor seal, harp seal, gray seal, ringed seal, crabeater seal and Weddell seal; odontocetes: bottlenose dolphin, common dolphin, Pacific white-sided dolphin, pilot whale, narwhal, beluga whale, sperm whale, Arnoux's beaked whale (*Berardius arnuxii*); mysticetes: humpback whale, fin whale, bowhead whale, and northern right whale. Data are from same sources as Fig. 5-25 with addition of Watkins et al. 1984, Würsig et al. 1984, Caldwell and Caldwell 1985, Hobson and Martin 1996.

analysis is consistent with the idea that phocids expend less energy than otariids to obtain a similar amount of prey. Lower existence costs may enable phocids to subsist on a poorer or more dispersed prey resource than otariids. The dramatic performance of northern fur seals also suggests that in the right circumstances, such as upwelling regions, otariids may be able to better use resources when prey is plentiful.

These differences in the pinniped foraging energetics suggest that phocids have a conservative foraging mode that can net similar amounts of energy to those obtained by otariids, but at significantly lower relative costs. Furthermore, the breeding pattern of phocid seals allows them to occupy habitats where productivity is lower (Costa 1993a). In contrast, otariids have a foraging and reproductive pattern that is energetically more costly, but appears to be optimal in highly productive regions where prey resources are not limited. This argument is consistent with pinniped distributions and global productivity. Otariids are only found in locations where productivity is high, whereas phocids breed in both the highly productive regions of the world and in areas of poorer productivity, like the Hawaiian Islands, the Mediterranean, and historically in the Caribbean.

There are interesting consequences if higher metabolic rates enable greater food acquisition when conditions are right. Predatory lizards that use a more costly, high activity, widely foraging behavior expend more energy. However, they may acquire proportionately more energy than lizards

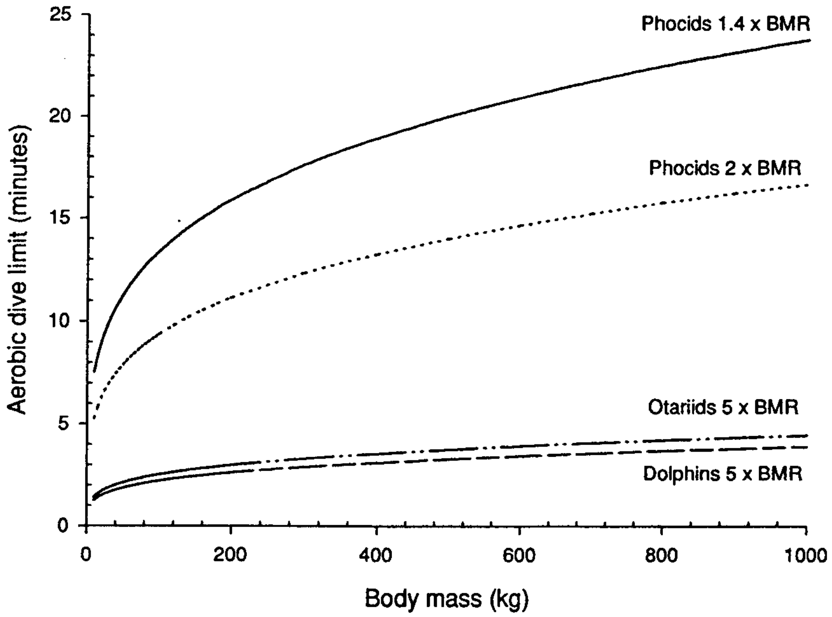


Figure 5-27. The variation in aerobic dive limit as a function of body mass calculated for a phocid seal operating at 1.4 and 2.0 times basal metabolic rate (BMR) and an otariid and a dolphin operating at 5 times BMR, respectively. Oxygen stores were assumed to be 60 mL O_2/kg for a phocid, 40 mL O_2/kg for an otariid, and 35 mL O_2/kg for a dolphin (Kooyman 1985).

Table 5-3. Dive Rate and Duration, Rate of Prey Energy Acquired, Energy Expenditure and Metabolic Rate of Two Otariids and a Phocid

Species/Diet	Mass (kg)	Dive Dive Rate (No. per day)	Dive duration (min)	Energy Acquired (kJ/min)	Energy Acquired (kJ/dive)	Energy Expended (kJ/min)	Energy Expended (kJ/dive	Ratio of Acquired/ Expended	Metabolic Rate FMR/BMR
Northern elephant seal Squid	350	65	19.2	1770	92	403	21	4	1.3
California sea lion Fish	85	202	2.0	224	112	52	26	4	4.8
Northern fur seal Squid	37	38	2.1	853	406	38	18	23	6.0

Data on prey intake were estimated from water influx and metabolic rate of the sea lion and fur seals from oxygen-18 doubly-labeled water measurements (Costa and Gentry 1986, Costa 1988a, Costa et al. 1991). Metabolic rate of northern elephant seal was estimated from dive behavior (Le Boeuf et al. 1988).

FMR/BMR = field metabolic rate/basal metabolic rate.

using a more economical, sit-and-wait foraging behavior (Anderson and Karasov 1981, 1988; Karasov and Anderson 1984; Nagy et al. 1984). An important consequence is that the widely foraging predators are able to devote more energy to reproduction than the sit-and-wait predators. Consistent with these findings is the observation that mammals with high metabolic rates reproduce faster than similar-sized mammals with lower metabolic rates (McNab 1980, 1983, 1984, 1986a,b). Such a pattern holds true when marine mammals are included in the analysis (Schmitz and Lavigne 1984). These arguments support the hypothesis that otariids expend more energy foraging, but they get more for their effort than phocids. This requires that sufficient resources be available to support such an expensive life style, but this is likely in the upwelling environments that otariids typically inhabit (Repenning and Tedford 1977, King 1983).

The Energetics of Prey Choice

The amount of work, and therefore, energy expenditure, that an animal puts into locating prey varies as a function of the energy content, availability, and location of the individual prey items. Both size and proximate composition (fat, carbohydrate, protein, and water content) affect the energy content of prey. Larger prey items or those with higher fat contents contain more energy. Fat contains almost twice as much energy per unit mass as protein or carbohydrate, and it is stored with significantly less water in body tissues. Prey availability varies as a function of the absolute abundance of prey (amount of prey per unit of habitat) and its distribution in the environment. This distribution dictates predator efficiency. A predator is more efficient foraging on prey that is clumped than on prey that is evenly dispersed. Marine mammals appear to forage in areas where prey has been concentrated as a result of oceanographic processes including eddies, fronts, and bottom topography (Costa 1993b; Bowen and Siniff, Chapter 9, this volume).

Because marine mammals must periodically return to the surface to breathe, the location or depth of the prey will determine how hard the animal must work at foraging. Deeper prey require greater swimming distances. Some prey may simply be beyond the animal's diving ability.

Because they forage in near-shore waters and are easy to observe, sea otters are excellent subjects for assessing variations in foraging behavior and ecology. Sea otters consume their prey on the water surface where it is easy to identify from shore. They generally forage in water depths that are easily reached by scientists using scuba gear, enabling the abundance and distribution of prey to be measured.

Sea otters select prey based on a combination of factors—energy content, its local abundance or availability, the time it takes to acquire and process it, and previous experience of the animal. In areas that have only recently been occupied by sea otters, the diet is made up almost exclusively of preferred prey items like clams, abalone, or sea urchins (Table 5-4). In these environments, sea otters find large, energy-rich, abundant prey, which is easy to handle, consume, and digest. In such situations lower quality prey items (turban snails, sea stars, mussels, chitons) generally do not appear in the diet. These items may be abundant, but are energy-poor and difficult to eat and digest. Abalone, clams, sea urchins, and crabs grow slowly. Therefore, sea otter foraging pressure rapidly causes a reduction in their abundance. As the abundance and size of their preferred prey items decline, sea otters switch to less preferred but more accessible prey items like turban snails, kelp crabs, and in some cases even chitons and sea stars (Table 5-4). Some sea otters specialize on different types of prey items (Riedman and Estes 1990). These specialists are more efficient predators on the selected prey than nonspecialists because of the foraging tactics involved. Turban snails are small and easy to find but require extended processing time; many small snails must be captured and the shells broken to get a decent meal. Nonetheless, snails are abundant throughout the kelp forest and are easy to locate. Conversely, abalone are found deep in rock crevices and use their muscular foot to hold firmly to the substrate. It usually takes an otter several dives to obtain one abalone, and it often requires the use of a rock to break the abalone's hold. Otters feeding on clams must learn how to dig them out of the mud or sand and how to break open their thick shells.

Polar bears represent another example of optimal prey choice and its relation to the prey energy quality. Feeding predominately on ringed seals, polar bears eat the energy-rich blubber layer and leave behind the lean "core" of the carcass. Because of its high lipid content, the blubber has a per unit mass energy content almost 10 times greater than that of the lean tissue of the seal (Stirling and McEwan 1975). More important, as mentioned above, fat retains relatively little water (approximately 10%) when it is deposited as blubber. This compares with protein and carbohydrate, which are stored with 70% to 80% water by mass (Kleiber 1975). Thus, polar bears have learned to consume the most energy-dense part of the ringed seal and then move on to find another kill (Stirling and McEwan 1975).

Fur seals and sea lions provide insight into the factors that govern prey choice of pelagic marine mammals. Fur seals are tied to shore for breeding and rely on the availability of nearby prey resources to produce milk for their young. Female fur seals must optimize the time they spend feeding at sea to the time spent nursing the pup onshore (Costa et al. 1989b; Costa 1991a,b; Lunn and Boyd 1993). Movements of foraging fur seals indicate that they have ranges near the breeding colony. Because fur seal and sea lion mothers periodically feed at sea and return to their pups onshore, they offer a tractable system to examine the foraging ecology of open-ocean marine mammals.

Northern fur seal females exhibit three different foraging patterns: they feed near the bottom over the continental shelf

Table 5-4. Foraging Behavior of Sea Otters in Central California

	Prey Energy Content (kJ)		Number of Prey Consumed		Proportion of Diet (%)	
Prey Item	Newly Occupied	Established	Newly Occupied	Established	Newly Occupied	Established
Kelp crab	—	207	—	58	—	49
Rock crab	761	761	3	11	28	9
Turban snail	—	90	—	108	—	15
Abalone	2908	607	9	12	69	10
Red sea urchin	971	27	—	19	—	14

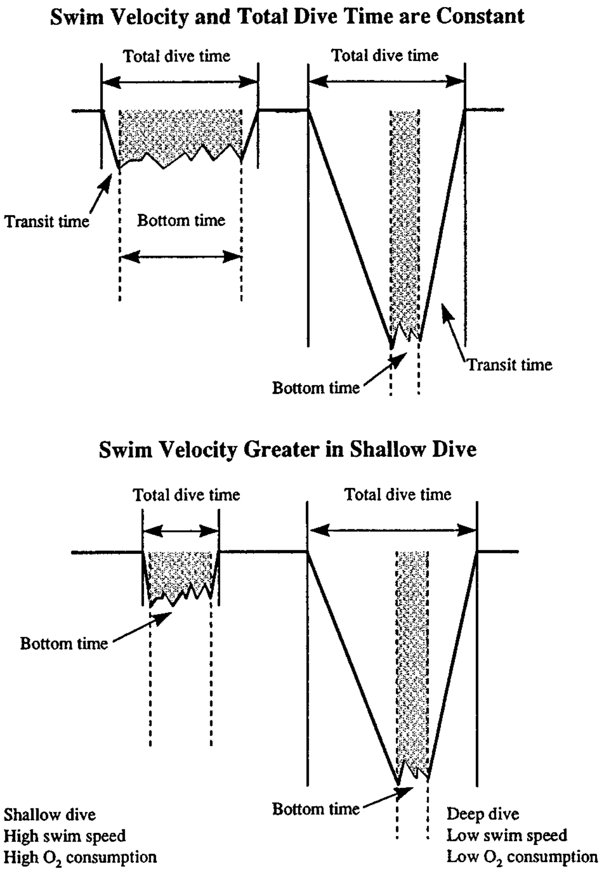
Data from Costa 1978.

where the depth seldom exceeds 200 m, over deep water off the continental shelf making only shallow dives, or they show a combination of deep and shallow dives (Loughlin et al. 1987). Deep-diving females apparently feed through the day and night on semidemersal juvenile walleye pollock that remain near the bottom (Sinclair et al. 1994). Females foraging over deep water beyond the continental shelf wait until gonatid squid (*Gonatopsis borealis* and *Berryteuthis magister*) and deep-sea smelt (*Leuroglossus schmidti*) move into shallow water before preying on them (Loughlin et al. 1987, Antonelis et al. 1993, Sinclair et al. 1994). The energetic difference between feeding on squid or pollock can be examined by comparing the total number of individual prey that would have to be captured per dive. Each individual pollock contains 10 times as much energy as each squid due to differences in both the energy density and size of individual prey (squid = 152 kJ, pollock = 1584 kJ) (Costa and Gentry 1986). Using estimates of the food requirements of foraging females and the total number of dives over a foraging trip, we find an average 695 kJ of prey energy obtained per dive when feeding on squid compared to 1500 kJ when feeding on pollock. A female fur seal would have to obtain five squid per dive compared to one pollock (Costa 1988b). Deep diving may only be economical when female fur seals feed on large prey that can supply a significant fraction of the energy requirement with each dive. Predation on small prey that require many individuals to be captured per dive is limited to shallow depths. However, one must be careful extrapolating these observations, as the terms shallow and deep are relative to the diving capability of the predator. Shallow to an elephant seal may be 300 m, whereas shallow to a northern fur seal is 30 m.

Some species feed exclusively on one type of prey. During the summer, Antarctic fur seals feed only on Antarctic krill. Nearly 75% of their night dives are shallower than 30 m. Daytime dives average 40 to 75 m (Croxall et al. 1985, Boyd and Croxall 1992). This pattern closely follows the vertical migration of krill, which remain below 50 m during the day and move near the surface at night. More than 40% of the krill are below 75 m depth at any time of day, but fur seal dives seldom exceed this depth. Although fur seals are physiologically capable of reaching this depth, it appears that it is too deep for them to efficiently feed on krill. Similar patterns have been observed for northern fur seals feeding on vertically migrating squid and other marine predators, such as macaroni (*Eudyptes chrysolophus*), chinstrap (*Pygoscelis antarctica*), and gentoo (*Pygoscelis papua*) penguins, feeding on krill (Croxall et al. 1988, Fraser et al. 1989).

What constraints account for these different foraging depths? Shallow dives use relatively little time in transit, leaving more time at the bottom of the dive to search for or pursue prey (Fig. 5-28). In contrast, deep dives require more time in transit, leaving less time to search for or pursue prey at the bottom of the dive. Thus, fewer prey can be obtained per long dive. If the same amount of time is spent per dive, and there is less time available to capture prey, it would be prudent to pursue prey of greater size and energy content. Likewise, if dives are of the same duration and prey is captured at a consistent rate per dive, more dives would be required when pursuing the prey of lower energy content. For short dives, increasing the number of sequential dives with a lower premium on energy return per dive would be the most economical strategy. For deep dives where transit time is long, a small number of long-duration dives with a high energy return per dive would be favored.

Faster swimming predators will use oxygen stores more rapidly and are limited to shallow dives or "spiked" dives with minimal bottom time (Fig. 5-28). In contrast, slow-swimming animals use oxygen less rapidly and make dives of longer duration. Presumably, the pursuit of many small prey


Swim Velocity and Total Dive Time are Constant

Swim Velocity Greater in Shallow Dive

Figure 5-28. The top portion of the figure presents schematic representations of the diving pattern for deep- and shallow-diving predators when oxygen utilization is constant and total dive durations are equivalent. The bottom figure demonstrates patterns when the rate of oxygen utilization is greater for shallow dives than for deep dives. In this case, total dive duration is not constant.

requires fast and agile swimming with high rates of oxygen consumption. Such a high rate of oxygen consumption would constrain the predator to many short dives. However, for a shallow-diving predator this may not be a serious constraint as transit time to foraging depth is brief and most of the dive can be spent in pursuit and acquisition of prey. The opposite is true for deep dives. If a deep diver were to swim fast, most, if not all, of the oxygen stores would be used in transit to and from depth with little left over for the search and pursuit of prey. Such a situation probably results in the "spiked" dives observed in many pinnipeds (Gentry et al. 1986, Le Boeuf et al. 1988, Crocker et al. 1994). By swimming slowly and reducing oxygen consumption, the predator gains bottom time at depth but probably is limited to feeding on slow-moving prey or prey that is only encountered occasionally. As a result, the predator should select large prey of high energy content. Flat-bottomed dives observed for deep-diving northern elephant seals (Le Boeuf et al. 1988) and New Zealand sea lions (Gentry et al. 1987, Gales and Mattlin 1997) are examples of marine mammals that use this strategy. The predator may also limit the pursuit phase to slow methodical swimming until the prey has been spotted and then switch to a rapid, energetically costly form of high-speed swimming. This strategy could limit the dive to a single capture before oxygen stores are depleted. If deep divers can only capture a few individuals per dive, then they should pursue prey containing the highest energy content.

Variations in Foraging Energetics

The foraging success of marine mammals declines as food resources change in response to their own foraging activities (Estes et al. 1978, Hines and Pearse 1982, Kvitek et al. 1992) or as a result of changes in local oceanographic or climatic conditions. Pelagic marine mammals may respond to changes in local food availability by migrating or moving to areas where conditions are optimal (Schoenherr 1991, Kenney et al. 1995, Whitehead 1996). Other species, like bottlenose dolphins in Sarasota Bay (Wells et al. 1987) or sea otters, exist in specialized habitats or have limited home ranges. If prey becomes depleted within their home range, they have a limited ability to move.

The relationship between prey availability and reproductive success has been examined for a wide variety of pinniped species. Otariids are more susceptible to variations in nearby food resources because their breeding pattern is linked to continuous prey availability directly offshore (Costa 1993a); phocids are buffered against fluctuations in prey availability near the rookery because they accumulate the resources they need for lactation over the previous year (Trillmich et al. 1991). Successful reproduction by otariids requires that mothers use a foraging pattern that optimizes the amount of time spent at sea feeding with the amount of milk energy delivered to her pup waiting on the rookery. Studies of female otariids with dependent young show that as food resources decrease mothers can either increase the time spent at sea foraging or they can increase the intensity of their foraging effort (Trillmich 1990, Costa 1991b, Trillmich et al. 1991). However, simply increasing the time spent at sea increases the time between visits to the pup. Consequently, more of the ingested milk energy is spent on pup maintenance rather than directed to pup growth. Increases in trip duration that are associated with declining prey resources result in slower pup growth because less milk is delivered over the same time interval (Oftedal et al. 1987, Costa and Croxall 1988, Croxall et al. 1988, Costa et al. 1989b, Trillmich et al. 1991, Lunn and Boyd 1993).

A more optimal strategy when faced with reduced prey is for otariid mothers to adjust their foraging behavior to keep the same attendance pattern and provide their pups with the same rate of milk delivery. This can be done by modifying foraging behavior by (1) spending more time at sea, (2) decreasing the time spent resting or in transit, (3) switching to more abundant, deeper, shallower, or higher energy-dense prey, or (4) increasing the intensity of their foraging effort by diving deeper, faster, and with a shorter surface interval. All of these responses have been observed in otariid mothers. Northern fur seal females responded to changes in prey availability by apparently changing both the type of prey consumed (Sinclair et al. 1994) and the intensity of their foraging effort (Costa and Gentry 1986). These fur seal mothers had significantly different FMRs without changes in trip duration or pup mortality (Costa and Gentry 1986).

In response to more severe reductions in prey availability associated with the 1983 El Niño event, California sea lions responded by changing prey and by increasing both their at-sea energy expenditure and trip duration (Costa et al. 1991, DeLong et al. 1991, Feldkamp et al. 1991). While at sea, sea lion mothers spent a greater percentage of total trip time diving (40.4% in 1982; 66.2% in 1983), exhibited diving bouts of longer duration (2.9 hr in 1982; 4.6 hr in 1983), made dives of greater duration (1.9 min in 1982; 2.6 min in 1983), and possibly dived to deeper depths as well as spent less time swimming (50.6% in 1982; 29.2% in 1983) and resting (4.1% in 1982; 1.5% in 1983) than pre-El Niño animals. These changes in behavior were accompanied by increases in the rate of energy expenditure at sea, which indicates that sea lions worked harder when prey was scarce (Costa et al. 1991, Feldkamp et al. 1991).

Some species of fur seals may have a limited capacity to accommodate changes in prey availability because they are prey specialists or are already foraging near maximum levels. In the South Georgia area of the South Atlantic Ocean, the Antarctic fur seal feeds almost exclusively on Antarctic krill, resulting in tight coupling of the reproductive success of the fur seals with local krill availability. Antarctic fur seals feeding on krill possess one of the highest at-sea metabolic rates; they are shallow divers and spend considerably more of their time at sea diving than other otariids examined to date. By operating close to their metabolic maximum, Antarctic fur seals have a limited ability to increase their foraging intensity and are less able to respond to reductions in prey availability without increasing the time spent away from their pups. During periods of poor krill availability, females increase the time spent foraging, the amount of activity while at sea, and the depth of their dives. These behavioral changes are insufficient to maintain a normal attendance pattern (Boyd et al. 1994) because Antarctic fur seal females appear to be working near their maximal metabolic effort even in normal years (Costa et al. 1989b, Costa 1991a). In response to variations in local prey resources, other fur seals and sea lions may choose different prey or have greater flexibility in their time-activity budgets than do Antarctic fur seals.

Phocids are buffered from short-term fluctuations in prey availability owing to their unique reproductive pattern. In phocids, reproductive performance (maternal investment) during a given season reflects prey availability over the preceding year and represents the mother's foraging activities over a much larger spatial and temporal scale than is the case for otariids (Trillmich and Ono 1991, Stewart and Lavigne 1984, Costa 1993a). It follows that the weaning mass of a phocid pup is an indicator of its mother's foraging success over the previous year (Stewart and Lavigne 1984), whereas the subsequent postweaning survival of the pup is related to both its weaning mass (energy reserves provided by the mother) and the resources available to the pup after weaning. Variations in the success of individual pups born during a single season have been observed for many ice-breeding seals. Reproductive rates in Weddell seals at McMurdo Sound exhibit 4- to 6-year fluctuations (Testa and Siniff 1987) that appear to be in phase with that of El Niño events. Changes in the occurrence of leopard seals (*Hydrurga leptonyx*) on sub-Antarctic islands associated with the proximity of the pack-ice edge (Rounsevell and Eberhard 1980) also correlate with El Niño events. Similar 4- to 5-year fluctuations in cohorts are evident in the age structure of crabeater seals (*Lobodon carcinophagus*) in the Antarctic peninsula (Bengtson and Laws 1983). These findings support the concept that large-scale oceanographic processes affect prey availability and thus population processes for many pinnipeds (Croxall and Rothery 1991, Testa et al. 1991).

Summary

It is apparent from this discussion that both intrinsic and extrinsic factors affect the flow of energy in marine mammals. Each species must balance the ability to acquire energy with the many avenues of energy expenditure. Energetic costs may range from supporting basal metabolic processes to providing for subsequent generations. These internal factors are not isolated from the environment in which the animal lives. Water temperature, seasonal changes, and oceanographic variables, among others, will influence both the physiology and the behavior of marine mammals. The appropriateness of the response by an animal challenged by these extrinsic factors will be manifest as an energetic cost or benefit. Ultimately, these will dictate the survivorship of the individual marine mammal as well as of the species.

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Killer Whale Predation on Sea Otters Linking Oceanic and Nearshore Ecosystems

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After nearly a century of recovery from overhunting, sea otter populations are in abrupt decline over large areas of western Alaska. Increased killer whale predation is the likely cause of these declines. Elevated sea urchin density and the consequent deforestation of kelp beds in the nearshore community demonstrate that the otter's keystone role has been reduced or eliminated. This chain of interactions was probably initiated by anthropogenic changes in the offshore oceanic ecosystem.

Apex predators often initiate forces that cascade across successively lower trophic levels, sometimes reaching the base of the food web (*1*). Plant-herbivore interactions vary predictably with trophic complexity in such systems, being weak or strong when the number of trophic levels is odd or even, respectively (*2*). Sea otters (*Enhydra lutris*) and kelp forests provide a well-known example of this pattern (*3*). After being protected from overhunting, recovering otter populations transformed nearshore reefs from two- to three-trophic-level systems by limiting the distribution and abundance of herbivorous sea urchins, thereby promoting kelp forest development (*4*).

Sea otters abounded across the North Pacific rim until unregulated exploitation in the maritime fur trade reduced the species to near-extinction by the early 20th century (*5*). Population regrowth began when protection was afforded under the International Fur Seal Treaty. A geographically discordant recovery pattern ensued because of the fragmented distribution of surviving colonies, the discontinuous nature of their habitat, and the otter's limited dispersal ability (*5*, *6*). Consequently, by the 1970s otter populations had recovered to near maximum densities in some areas of their historic range, were growing rapidly in others, and remained absent from still others (*7*). The sea otter's predatory role in kelp forest ecosystems was discovered by contrasting inhabited with uninhabited areas (*8*) and by observing changes over time as the uninhabited areas were recolonized and their founding populations grew (*4*, *9*). In addition to showing the influence of sea otters on North Pacific kelp forests, this approach has demonstrated a breadth of indirect effects on coastal ecosystems (*10*). The sea otter's reputation as a keystone species (*11*) is based on these interactions and processes.

Recently, sea otter populations have declined precipitously and unexpectedly over large areas of western Alaska. We first detected this decline through population surveys at Adak Island in the central Aleutian archipelago, which indicated that the otter population decreased ~25% per year through the 1990s, resulting in nearly an order-of-magnitude overall reduction by 1997 (Fig. 1). Additional surveys of Little Kiska, Amchitka, and Kagalaska Islands all show population declines of similar timing and rate to that which occurred at Adak (Fig. 1). Aerial surveys of the Aleutian archipelago conducted by the U.S. Fish and Wildlife Service in 1965 and 1992 further indicate that these declines are occurring throughout the region (*12*). The concurrent and widespread nature of these declines strongly suggests a causal link with the oceanic environment.

Demographic explanations for the sea otter population declines are limited to reduced fertility, increased mortality, or redistribution. Of these, reduced fertility and redistribution can be excluded. Studies of radio-tagged sea otters at Amchitka Island in 1992–94 and Adak Island in 1995–96 show that birth rates of adult females and pup survival rates from birth to weaning were similar to those of stable populations. Redistribution is equally unlikely because the declines were synchronous over large areas—there have been no population buildups on some islands to account for the losses on others—and radio-tagged otters at Amchitka and Adak islands provided no indication of redistribution during the declines (*13*). From this we conclude that the sea otter population declines were caused by increased mortality.

Three lines of evidence point to increased predation by killer whales (*Orcinus orca*) as the reason for this mortality. First, although killer whales and sea otters have been observed in close proximity for decades, the first attack on a sea otter was seen in 1991. Subsequently, nine more attacks have been reported (*14*). We evaluated the likelihood that this cluster of recent observations was due to chance alone by summing the number of person-days spent in the Aleutian Islands by our research team before and after 1990 (3405 person-days before; 4005 after), estimating the attack rate from the post-1990 data (0.0015 attacks per day), and then calculating the probability of no attacks being seen before 1990 if the attack rate remained constant over the 27-year period. By modeling the expected number of observed attacks as a Poisson process, the probability of zero attacks being seen before 1990 is 0.006 (*15*).

Second, we evaluated the impact of killer whales on sea otter populations at Adak Island by contrasting otter population trends and survival rates between Clam Lagoon, an area uniquely inaccessible to killer whales, and adjacent Kuluk Bay, an open coastal environment (Fig. 2). Sea otter numbers were stable from 1993 through 1997 in Clam Lagoon, whereas in Kuluk Bay they declined by 76%. In 1995, we marked 17 otters in Clam Lagoon and another 37 in Kuluk Bay with flipper tags and surgically implanted radio transmitters in order to compare their behavior and demography. There was virtually no movement of the marked animals between these areas. However, through year 1 of the study, the disappearance rate of sea otters in Kuluk Bay (65%) was greater than five times that of Clam Lagoon (12%), a trend that continued through year 2.

Finally, we estimated how many otters must have been eaten by killer whales to drive the decline rates, and then compared the actual number of observed attacks with the expected number of observed attacks based on this estimate. This analysis was done for the area between Kiska and Seguam Islands. Before the onset of the decline, an estimated 52,656 otters inhabited this area (*16*). Life table statistics (age-specific birth and death rates) were estimated from data collected during earlier field studies to construct a Leslie matrix for a stationary population. We then added an age-constant death rate (*17*) from killer whale predation sufficient to reduce the population by 78% over 6 years—the observed rate and magnitude of decline at Adak. The simulation was run by holding the number of individuals that died from killer whale predation constant over time, which produced a loss estimate of 6788 otters per year. The expected number of observed attacks produced by this approach is 5.05 for this 6-year period (*18*). This compares favorably with the 6 attacks that were seen.

Disease, toxins, and starvation, which are three other causes of elevated mortality in wildlife populations, can be dismissed as causes of the population declines. Any one of these should have produced substantial numbers of beach-cast carcasses, whereas very

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few were found. Marked increases in sea urchin biomass during the population decline at Adak (Fig. 1) are further evidence against starvation, because sea urchins are the principal prey of sea otters in the Aleutian Islands (*19*). Although we looked specifically for signs of disease, none were found (*20*). Elevated contaminant concentrations have been reported in the Aleutian Islands (*21*), but subsequent analyses from 39 sites across the Aleutian archipelago have shown that these are restricted to a few small areas (*22*), which is inconsistent with the widespread declines in otter numbers.

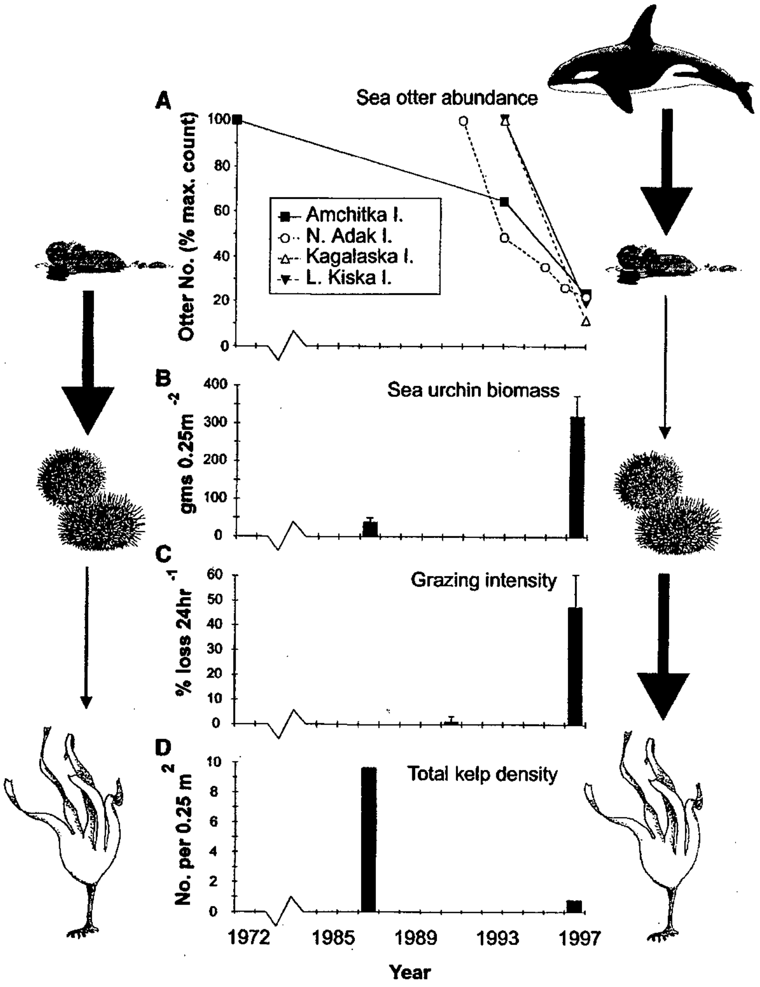

Fig. 1. (**A**) Changes in sea otter abundance over time at several islands in the Aleutian archipelago and concurrent changes in (**B**) sea urchin biomass, (**C**) grazing intensity, and (**D**) kelp density measured from kelp forests at Adak Island. Error bars in (B) and (C) indicate 1 SE. The proposed mechanisms of change are portrayed in the marginal cartoons—the one on the left shows how the kelp forest ecosystem was organized before the sea otter's decline and the one on the right shows how this ecosystem changed with the addition of killer whales as an apex predator. Heavy arrows represent strong trophic interactions; light arrows represent weak interactions.

The collective evidence thus leads us to conclude that increased killer whale predation has caused the otter declines. Although the population size and status of killer whales in the Aleutian Islands are unknown, these animals are commonly seen. From the energetic requirements of free-ranging killer whales and the caloric value of sea otters, we estimate that a single killer whale would consume 1825 otters per year and thus that the otter population decline could have been caused by as few as 3.7 whales (*23*).

Strikingly rapid changes in the kelp forest ecosystem have accompanied the sea otter population declines (Fig. 1). In 1987, when otters at Adak Island were near equilibrium density, the kelp forests were surveyed at 28 randomly selected sites (*4*). Otters were still numerous at Adak in 1991, when five of these sites were randomly chosen for the measurement of plant tissue loss to herbivory (*24*). Using similar procedures at the same sites in 1997, we resurveyed the kelp forest and repeated the measurements of plant tissue loss to herbivory. Over the 10-year interim, sea urchin size and density increased to produce an eight-fold increase in biomass, while kelp density declined by more than a factor of 12 (Fig. 1). The average rate of kelp tissue loss to herbivory increased from 1.1% per day in 1991 to 47.5% per day in 1997 (Fig.1). Observations made in August of 1997 revealed similar changes at Kiska, Amchitka, and Kagalaska Islands.

Killer whales and sea otters have co-inhabited the west-central Aleutian archipelago for much of the past half century, and probably for millennia before. Thus, it is necessary to ex-

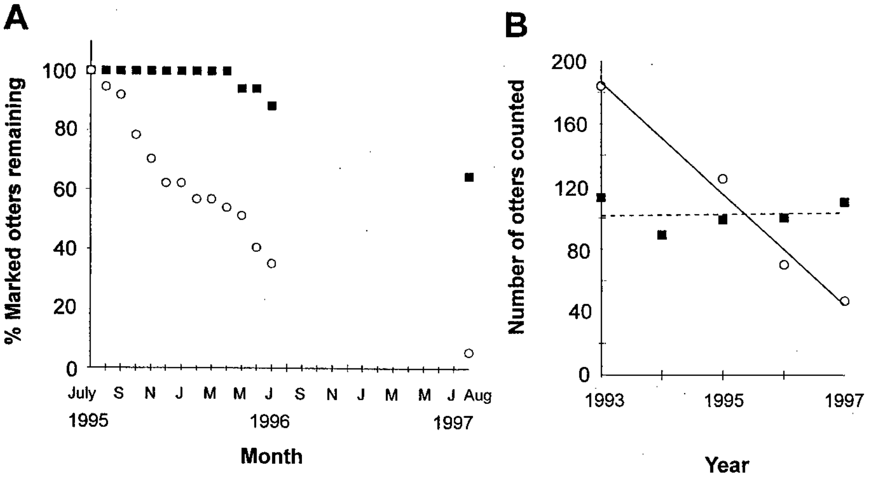

Fig. 2. Population trends and survival rates of sea otters in Clam Lagoon (solid squares) and adjacent Kuluk Bay (open circles), Adak Island, Alaska. (**A**) The rate of population change r, calculated as the slope of the linear best fit to the natural log of the number of otters counted versus year, for Kuluk Bay between 1993 and 1997 was -0.345 (SE = 0.058), which is significantly different from 0 ($R^2 = 0.946$, $P = 0.027$). In Clam Lagoon, the rate of change over this same period was 0.006 (SE = 0.034), which is not significantly different from 0 [$R^2 = 0.011$, $P = 0.867$; statistical power to detect $r \geq 0.1 = 0.9$]. The measured rates in Kuluk Bay and Clam Lagoon differed significantly ($\chi^2 = 27.26$, 1 df, $P < 0.001$). (**B**) Survival rates of marked sea otters differed significantly between Clam Lagoon (0.88 year^{-1}) and Kuluk Bay (0.35 year^{-1}; $\chi^2 = 13.52$, 1 df, $P < 0.001$).

plain why the behavior of killer whales toward sea otters has recently changed. The most likely explanation is a shift in the prey resource base for killer whales. Some killer whale groups or individuals feed on marine mammals (*25*), including Steller sea lions and harbor seals, and populations of both these species recently have collapsed across the western North Pacific. Sea lion populations began to decline in the late 1970s, and their numbers had reached minimum levels in the Aleutian islands by the late 1980s (*26*), a time that coincides with the onset of otter declines. Although the exact cause of the pinniped decline is uncertain (*27*), it probably relates to reduced abundance and altered species composition of their prey (*28*). Recent population declines of piscivorous marine birds are consistent with this explanation (*29*). Why forage fish stocks have shifted is not well understood, although the change was likely caused by some combination of effects from the region's burgeoning fisheries, increased ocean temperature, and depletion of baleen whales (*30*).

Regardless of the ultimate cause, sea otter population declines and the consequent collapse of kelp forest ecosystems almost certainly have been driven by events in the offshore oceanic realm. Our proposed explanation involves a chain of ecological interactions, beginning with reduced or altered forage fish stocks in the oceanic environment, which in turn sent pinniped populations into decline. Pinniped numbers eventually became so reduced that some of the killer whales who once fed on them expanded their diet to include sea otters. This shift in killer whale foraging behavior created a linkage between oceanic and coastal ecosystems and in so doing transformed coastal kelp forests from three- to four-trophic-level systems, thereby releasing sea urchins from the limiting influence of sea otter predation. Unregulated urchin populations increased rapidly and overgrazed the kelp forests, thus setting into motion a host of effects in the coastal ecosystem.

Parts of this scenario are well documented, others are more speculative, and still others have yet to be evaluated. Nonetheless, the data are sufficient to make several points of broader ecological significance. First, our findings afford evidence of the often underappreciated importance that uncommon and transient species can have in controlling community structure, demonstrating further that such species can link interactions across ecosystems. Although intersystem linkages are becoming increasingly well known (*31*), this example is unusual because the linkage is formed through the activities of a top-level carnivore. Additionally, our results are relevant to understanding food web dynamics, because they demonstrate that adding another apex predator to a system under top-down control has predictable effects on plant populations at the base of the food chain. Finally, results from this long-term study have implications for both the approach to and scale of other ecological field studies. The events reported here could not have been chronicled or even detected in a short-term study, were unanticipated, and thus seem poorly suited for analysis by a priori hypothesis testing. These points emphasize the potential significance of large-scale ecological events and the consequent need for large-scale approaches in ecological research.

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12. By 1965, otter populations had recovered to pre-exploitation levels at most of the Aleutian islands, from Kiska in the west to Adak in the east (*5*). Of the 21 islands in this region that were surveyed in both 1965 and 1992, sea otter counts decreased at all but one, for an average reduction of 58%. The 1965 data are from (*5*); the 1992 data are from T. J. Evans *et al.*, *Technical Report MMM 97-5* (U.S. Fish and Wildlife Service, Anchorage, AK, 1997).
13. Among resightings of radio-tagged otters at Adak (1635 resightings of 52 otters) and Amchitka (3711 resightings of 98 otters), the maximum distances moved were 4.31 and 6.95 km, respectively. From 1992 to 1997, most of the marked animals that were lost from these populations disappeared suddenly and without a trace, after being seen regularly in predictable locations through months of study.
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15. This probability was calculated from the Poisson probability density function $f(x) = e^{-\mu}\mu^{x}/x!$, for μ = 5.1 (the expected number of attacks seen) and $x = 0$ (the number of attacks actually seen).
16. This number was obtained from counts made during a 1965 aerial survey (*5*) and adjusted upward by a factor of 5.62 to account for the proportion of animals that were not seen. The adjustment factor was calculated from a 1972 estimate of sea otter abundance at Amchitka Island [estimate, 6432; from J. A. Estes, in *The Environment of Amchitka Island*, M. L. Merritt and R. G. Fuller, Eds. (TID-26712, U.S. Energy Research and Development Administration, Springfield, VA, 1977), pp. 511–526] divided by the number of otters counted at Amchitka in the 1965 aerial survey (1144).
17. The age-constant death rate was inferred from the age-constant rates of otter disappearance seen in our field studies of marked sea otters at Adak Island.
18. The expected number of observed attacks was calculated as $N(t/T)(a/A)$, where N = 40,728 otters, which is the estimated number eaten by killer whales between 1991 and 1997; t = 21,677 hours, which is the number of person-hours of field time spent by our research team during this period; T = 52,560 hours (that is, 6 years); a = 1 km, which is the observer's sighting window [that is, two times the maximum distance from observers that attacks have been seen (*14*)]; and A = 3327 km, which is the area's coastal length.
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23. We have estimated that 40,000 sea otters would have to have been eaten to drive the observed decline. The minimal number of killer whales necessary to consume this number of otters was determined by measuring the caloric value of sea otters; estimating the field metabolic rate of killer whales, discounted for assimilation efficiency; and then equating these values to estimate the number of sea otters needed to fuel a wild killer whale. The caloric content of adult sea otters, determined by adiabatic bomb calorimetry of homogenized carcasses, averaged 1.81 ± 0.04 kcal gm^{-1} of wet weight. Field metabolic rate (FMR) was 7934 watts (W) for female and 11,800 W for male killer whales (51 t 59 kcal kg^{-1} of killer whale per day). Values for FM were based on field metabolic rates of odontocete (D. P. Costa and T. M. Williams, unpublished data) an their basal metabolism [B. Kriete, thesis, Univ. of Britis Columbia (1995)]. Our estimate of killer whale FM compares with the 30 to 62 kcal kg^{-1} day^{-1} reported b L. G. Barrett-Lennard *et al.* [*Report for the North Pacifi Universities Marine Mammal Consortium* (Univ. o British Columbia, Vancouver, BC, Canada, 1994) R. W. Baird [thesis, Simon Frasier University, Vancouver, BC, Canada, (1994)], and B. Kriete [thesi Univ. of British Columbia, Vancouver, BC, Canad (1995)]. The caloric value of sea otters compare with a range of 0.78 to 3.55 kcal gm^{-1} of we weight for fish and other marine mammals th make up the killer whale diet. An adult male se otter weighing 34 kg provides 61,540 kcal (34,00 gm × 1.81 kcal gm^{-1} of wet weight); a 23-kg adu female otter provides 41,630 kcal. From this, w calculated that an adult female killer whale feedi exclusively on sea otters would need three male five female sea otters per day, and an adult ma would require five male or seven female otters p day. The average consumption rate (five otters p whale per day) was divided into the sea otter lo estimate to determine how many killer whal would be needed to account for the losses. Bas on this approach, 3.7 killer whales feeding excl sively on sea otters would be sufficient to drive t population decline.
24. These measurements of plant tissue loss were o tained by placing preweighed pieces of tissu from blades of the four most common kelp sp cies—*Alaria fistulosa*, *Laminaria groenlandica*, *Ag rum cribrosum*, and *Thalassiophyllum clathrus*— the seafloor and recording their change in m over 24 hours relative to that of adjacent cag controls. Five replicates were done for each spec at each site.
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COVER Killer whales in the North Pacific. Recently increased predation by these apex predators has driven sea otter populations sharply downward, thus creating an ecological chain reaction in nearshore ecosystems. Dwindling harbor seal and Steller sea lion populations apparently induced killer whales to begin eating large numbers of sea otters. [Photo: G. Ellis]

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CHAPTER 2

Strategies for reducing foraging costs in dolphins

T.M. Williams, S.F. Shippee and M.J. Rothe

SUMMARY

(1) **The major energetic costs faced by an aquatic endotherm include those associated with maintaining basal metabolism, thermoregulation, locomotion, and digestion.**

(2) Wave-riding, intermittent modes of swimming, and limiting transit swimming to maximum **range speeds reduce the cost of locomotion and increase the time available for foraging in the diving dolphin.**

(3) Energetic costs associated with high speed ascent and descents, and thermoregulation (if not compensated for by locomotor thermogenesis) result in significant decreases in the time available for foraging by diving dolphins.

(4) Behaviours that dolphins use to reduce locomotor and thermoregulatory costs can benefit the foraging animal by conserving limited oxygen reserves during a dive. As a result, a greater proportion of the reserve will be available for predator–prey interactions.

Key-words: aquatic predation, bottlenose dolphin, diving, energetics, *Tursiops truncatus*

INTRODUCTION

Many conventional foraging models for aquatic predators maximize the net rate of energy intake over the period of foraging (Stephens & Krebs 1986, Kramer 1988). Important elements of these models include:

(1) energetic costs defined as the amount of energy expended to perform a particular behaviour,
(2) energetic benefits defined as the amount of energy gained by performing the behaviour, and
(3) the time required for these behaviours.

The latter element is especially critical for aquatic mammals in which the duration of a foraging dive is dictated by the parsimonious utilization of oxygen stores. For these animals the costs and benefits of foraging must be balanced against limited oxygen reserves in the muscles, blood and lungs (Dunstone & O'Connor 1979, Williams *et al.* 1993b).

There has been considerable effort in detailing the energetic benefits of foraging in aquatic mammals. For example, prey consumption and diets have been described for sea otters (Riedman & Estes 1990), pinnipeds (Condit & Le Boeuf 1984, Gentry *et al.* 1986), and dolphins (Barros & Odell 1990, Cockcroft & Ross 1990, Hanson & Defran 1993). In contrast, comparatively little is known about the various energetic costs associated with foraging by aquatic mammals. Often these costs are averaged in a field metabolic rate obtained from the doubly-labelled water method (Costa 1991).

The major energetic costs faced by foraging endothermic swimmers include the energy expended for basic biological functions, thermoregulation, locomotion (swimming and diving), and digestion (heat increment of feeding and the cost of heating ingested prey). These costs are incorporated in the travel, search, pursuit and handling costs typically used in ecological models of foraging (see Charnov 1976, Stephens & Krebs 1986). Our focus is on the physiological rather than behavioural capabilities of the animal. Furthermore, in our model individual energetic costs may not always be mutually exclusive, whereas in the ecological models they necessarily are. For example, locomotor activity may offset thermoregulatory demands (see below). The non-exclusive nature of these costs means that the combined effects of the various energetic costs must be considered when assessing the total cost of foraging by an animal.

During the past five years, we have conducted a series of physiological studies to determine energetic costs in the bottlenose dolphin *Tursiops truncatus*. This paper is our first attempt to apply these measurements to foraging theory. We examine the individual energetic costs associated with a simulated foraging dive and estimate their effect on oxygen reserves, and hence foraging time in these animals.

MATERIALS AND METHODS

Adult dolphins (average body weight = 145 kg) were trained to rest in a metabolic chamber (n = 3 males and 3 females, Williams *et al.* 1992b), swim next to moving boat (n = 1 male and 1 female, Williams *et al.* 1992a), and dive to submerged targets (n = 1 male and 2 females, Williams *et al.* 1993b). Ascent and descent rates, heart rate and behaviour during diving were monitored with microprocessors (Wildlife Computers, Inc.) placed on a pectoral fin strap or on a body harness. Measurements of oxygen consumption, heart rate and blood lactate for resting and active dolphins were used to determine the energetic cost of each activity. These costs were then used to compare the energetic consequences of basal metabolism, locomotor mode and thermoregulation during a dive. By defining the various energetic components of diving, we were able to identify behaviours that would enable the aquatic mammal to reduce costs associated with travelling between prey patches or between the water surface and depth.

RESULTS AND DISCUSSION

Maintenance and thermoregulatory costs

Maintenance costs and thermoregulatory costs were determined from the metabolic rate of bottlenose dolphins resting in water ranging from 3.6°C to 17.3°C (Williams *et al.* 1992b). The experiments were conducted on adult animals acclimated to ambient water temperatures of 15°C in San Diego (California) or 25°C in Kaneohe Bay (Hawaii). The results of the study showed that basal metabolism and lower critical temperature of the dolphins depended on acclimation temperature. Animals acclimated to 15°C had a basal metabolic rate that was 1.4 times the value measured for dolphins acclimated to 25°C. Lower critical temperature was less than 6°C for the cold acclimated dolphins and 11–16°C for the animals living in warm water. Thus, both acute and chronic changes in water temperature altered total energetic costs in the dolphin.

Several behaviours will enable a foraging dolphin to maintain low maintenance and thermoregulatory costs. These include limiting foraging excursions to areas where water temperatures are within the thermal neutral zone, and recycling heat generated by locomotor movements. Thermogenic muscular activity has been demonstrated for other aquatic and semi-aquatic mammals, and may be important for small cetaceans that live in cold seas. Swimming minks show a complex balance of locomotor heat production, body temperature and heat storage. Increased heat production during high speed swimming can offset thermoregulatory demands and stabilize the core body temperature of these small mammals (Williams 1986). Likewise, active sea otters (Costa & Kooyman 1984) and California sea lions (T. Williams, unpublished data) can compensate for thermoregulatory costs when moving or swimming at speeds as low as 1 m $\cdot$ s^{-1}. Further studies are needed to determine the magnitude of thermogenic muscular activity in cetaceans and its effect on total energetic costs.

Locomotor costs

Swimming and diving represent major energetic expenditures in aquatic mammals. In wild bottlenose dolphins, locomotor activities comprise more than 82% of the animal's daytime activity budget (Hanson & Defran 1993). The energetic costs of these activities have been examined in ocean-trained bottlenose dolphins. Williams *et al.* (1992a) investigated the swimming energetics of two adult dolphins trained to match their swimming speed with that of a 22 ft Boston whaler. Acoustic signals were used to position the dolphins 5–15 m amidships from the boat out of the wake zone. The results from this study demonstrated that the transport costs for adult dolphins swimming at various speeds (Fig. 2.1) showed a U-shaped curve typical of other swimming mammals (Williams 1983, Davis *et al.* 1985). No significant difference

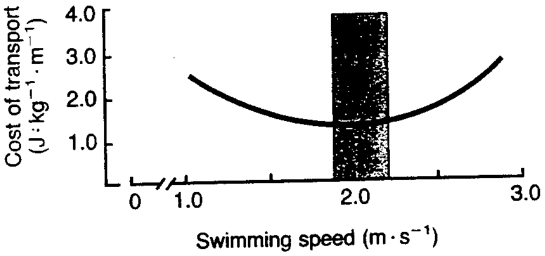


Fig. 2.1. Cost of transport in relation to transit speed for swimming bottlenose dolphins. The curve was calculated from values of oxygen consumption determined for two adult dolphins swimming next to a moving boat. The shaded area denotes the routine cruising speeds of coastal dolphins (Würsig & Würsig 1979) and corresponds to the predicted speeds for maximum range (redrawn from Williams *et al.* 1993a).

in heart rate, blood lactate or swimming energetics were observed for similarly sized male and female dolphins. The minimum cost of transport was 1.29 ± 0.05 $\mathrm{J \cdot kg^{-1} \cdot min^{-1}}$ and occurred at a swimming speed of 2.1 $\mathrm{m \cdot s^{-1}}$. The theoretical maximum range speeds, those swimming speeds that allow the animal to achieve the greatest distance per unit power input, were 1.7 to 2.3 $\mathrm{m \cdot s^{-1}}$ for these dolphins.

Two behavioural strategies, wave-riding and utilization of maximum range speeds, enable dolphins to reduce the energetic cost of transit swimming. Transport costs for wave-riding dolphins moving at 3.8 $\mathrm{m \cdot s^{-1}}$ are similar to those of freely swimming dolphins moving at 2.1 $\mathrm{m \cdot s^{-1}}$. This behaviour enables the dolphin to achieve comparatively high transit speeds at a relatively low cost. In the absence of wave-riding, dolphins can maintain low transport costs by selecting swimming speeds between 1.7 and 2.3 $\mathrm{m \cdot s^{-1}}$, that is, the maximum range speeds (Fig. 2.1).

Diving dolphins may also use burst-and-glide swimming to reduce locomotor costs. We designed an experiment in which bottlenose dolphins were trained to dive in a straight line path to submerged targets. The targets were placed at 54 m depth to simulate a relatively easy dive, and at 206 m to test a depth at which oxygen stores may become limiting. Total oxygen reserves had been determined previously and were 33 $\mathrm{mlO_2 \cdot kg^{-1}}$ body weight for adult bottlenose dolphins (Williams *et al.* 1993b).

Rather than swim at the maximum range speeds, the dolphins descended slower and ascended faster than predicted for transit swimming. Total energetic cost for a 206 m dive with a mean descent rate of 1.5 $\mathrm{m \cdot s^{-1}}$ and mean ascent of 2.5 $\mathrm{m \cdot s^{-1}}$ was 42.2 $\mathrm{mlO_2 \cdot kg^{-1}}$ as calculated from the swimming costs in Figure 2.1. These calculations assumed that the diving dolphin used constant propulsion. The result was a total energetic cost for diving that exceeded the animal's oxygen stores by nearly 30%. Subsequent video sequences of the dives showed that the dolphins switched from constant propulsion to an intermittent mode of swimming during the ascent from longer dives. More than 70% of the ascent period was spent gliding. If we account for the lower metabolic cost of the glide sequences, then the energetic cost of the 206 m dive is reduced by 6.2 $\mathrm{mlO_2 \cdot kg^{-1}}$ and remains within 10% of the animal's total oxygen reserve.

Digestive costs

The energetic costs associated with ingesting food have not been examined in bottlenose dolphins. However, the heat increment of feeding and the warming of ingested prey represent important energetic expenditures in a variety of aquatic predators. In the smallest species of marine mammal (sea otter, *Enhydra lutris*) and species of penguin (little blue, *Eudyptula minor*), the calorigenic effect of digestion plays an important role in the thermal balance of the resting animal. The metabolic rate of sea otters resting in water may increase by 54% following feeding (Costa & Kooyman 1984). Baudinette *et al.* (1986) found that the rates of oxygen consumption of the fed little blue penguin resting in air was 1.9 times the mean value of the post-absorptive bird. These elevated metabolic rates associated with digestion and termed the heat increment of feeding or specific dynamic action, coincided with a decrease in thermogenic muscular activity. In addition, the cost of heating ingested prey led to significant increases in the resting metabolism of marine birds (Wilson & Culik 1991) and mammals (Davis & Williams 1992). Food-induced thermogenesis may also enable small seabird species to forage in northern temperate and arctic oceans (Croll & McLaren 1993).

Strategies for reducing energetic costs during diving

Small cetaceans display a wide variety of foraging methods that vary in energetic cost. In relatively shallow water (<60 m) with sandy substrates, bottlenose dolphins will hold station quietly, head down, presumably echolocating on buried prey (D. Herzing, personal communication; T. Williams, unpublished data). Detected prey items are subsequently captured after digging through the sand with their rostrum (Fig. 2.2). Several fish may be taken on a single dive. Dolphins

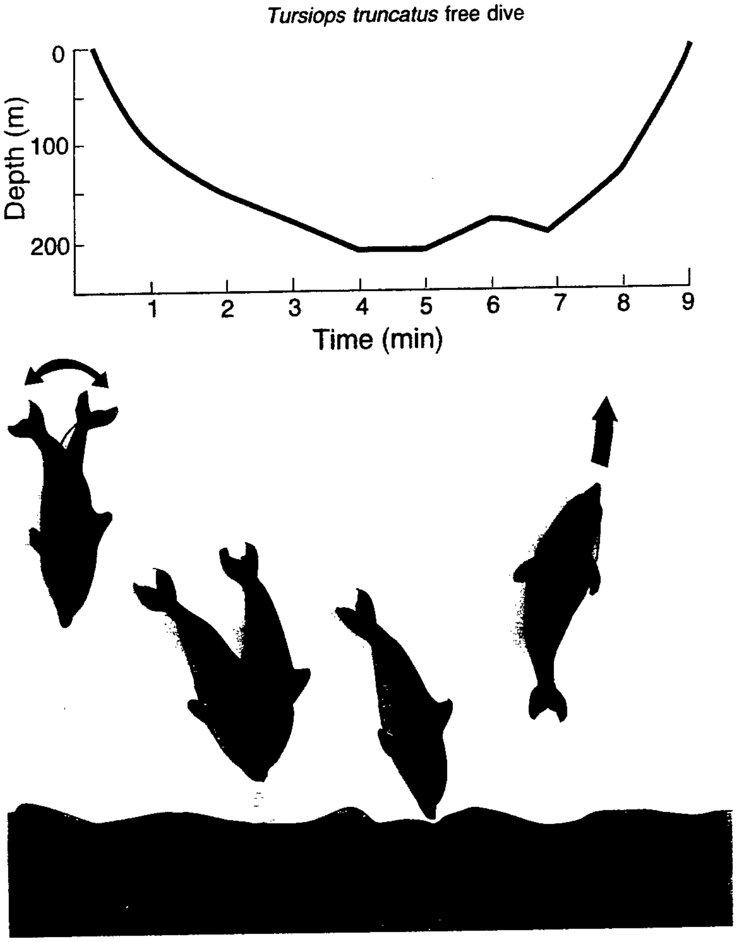
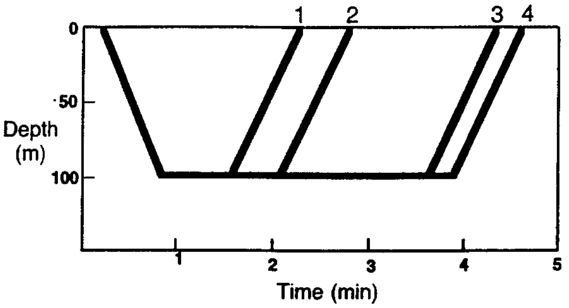


Fig. 2.2. Foraging behaviour in the bottlenose dolphin. The upper portion of the figure illustrates a typical dive profile (depth in relation to time) from a foraging dolphin carrying a time/depth microprocessor. The lower portion of the figure shows one type of foraging behaviour in which dolphins use echolocation to detect buried prey items.

will also herd fish into shallow areas (Shane 1990), or as seen with spinner *Stenella longirostris* and spotted dolphins *S. plagiodon*, allow fishing operations to herd the fish for them (Allen 1985, Pryor *et al.* 1990). For coastal populations of bottlenose dolphins, chases involving prey items are often of short duration and are associated with aggregations of fish or physical features (reefs, shallow water) that limit fish movements (Cockcroft & Ross 1990, Shane 1990). Feeding by coastal bottlenose dolphins in San Diego has been characterized by frequent steep and rapid dives (Hanson & Defran 1993).

We can begin to understand how individual energetic costs may affect foraging in bottlenose dolphins by examining the search dive. These dives consist of descent, bottom and ascent phases (Fig. 2.3). For comparative purposes, we will assume that the dolphin is relatively quiescent during the bottom phase, as may occur with slow transits between prey patches or predictable, non-mobile prey. This phase will necessarily be shorter if the animal is active while at depth, but will not be addressed here. We also assume that the animal attempts to maximize bottom time which in turn allows it to increase the time spent in locating, pursuing, capturing and handling prey. Maximum dive time is dictated by a reserve of $33\,\mathrm{mlO_2 \cdot kg^{-1}}$ body weight for dolphins that must be replenished when the animal surfaces to breathe.

The various energetic costs deplete the oxygen reserve in accordance with metabolic demands. This places limits on the amount of oxygen available for supporting the bottom phase. For instance, if a dolphin uses the predicted maximum range speed of $2\,\mathrm{m \cdot s^{-1}}$ for ascent and descent on a 100 m dive, its metabolic rate is $8\,\mathrm{mlO_2 \cdot kg^{-1} \cdot min^{-1}}$ (Williams *et al.* 1992a) during transit phases lasting 50 s each. Total cost for the



Dive strategy	Foraging time (min)
1 High speed ascent/descent	0.8
2 Winter metabolism	1.3
3 Optimum swim speed	2.6
4 Burst and glide ascent	2.8

Fig. 2.3. The effect of diving strategy on bottom (foraging) time in bottlenose dolphins. Upper portion of the figure shows a schematic profile for a 100 m search dive. In this model, foraging time is equivalent to bottom time (horizontal portion of the dive profile). Listed numbers for each strategy correspond to the timing of the ascent phase of the dive and the coincident bottom time.

ascent and descent phases is $13.3\,\mathrm{mlO_2 \cdot kg^{-1}}$; the remaining oxygen store will support a quiescent bottom time of 2.6 min. If the dolphin uses burst-and-glide swimming on the ascent, metabolic rate during the ascent is reduced by approximately 20% and bottom time concomitantly increases to 2.8 min.

High speed ascent and descents, and elevated thermoregulatory costs, if not compensated for by locomotor thermogenesis, will reduce bottom time in diving dolphins. Bottom time is less than 60 s if the animal swims at $3.0\,\mathrm{m \cdot s^{-1}}$ when travelling between the water surface and depth. This reduction is due to the prohibitively high transport costs associated with high speed swimming (Fig. 2.1). Thus, to move quickly between resources (i.e. oxygen at the water surface and submerged prey) the animal must bear a marked reduction in foraging time. Although an energetically costly strategy when searching for prey, high speed movements may be advantageous once prey that is patchy in distribution and ephemeral in time has been identified.

Maintaining an elevated metabolic rate to compensate for cold water temperatures or warming ingested prey also limit bottom, and therefore foraging, time for the dolphin (Fig. 2.3). Such limitations may be avoided by thermogenic muscular activity, but require further research in cetaceans. It is likely that the relationships between locomotor heat production, thermoregulatory demands, digestive costs and prey availability will be important factors in determining the range of foraging in wild populations of dolphins (Wells *et al.* 1990).

In view of the above discussion, behaviours that dolphins use to reduce locomotor and thermoregulatory costs can benefit the foraging animal by conserving limited oxygen reserves during a dive. As a result, a greater proportion of the reserve will be available for potential predator–prey interactions. An unknown component of our energetic model is the net rate of energy gained when using these different behavioural strategies. This becomes evident over a series of dives rather than the single event examined here, and awaits investigation.

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